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### Errata

- P. 518, Fig. 8. *For 18-17-31-1 read 18-17-35-1*
- Pp. 511, 512, 520. *For Fabonacci read Fibonacci*

## Starch formation in the leucoplasts of *Phaseolus vulgaris*

PAULINE YOUNG

(WITH PLATE 1)

It is generally assumed that, in the transformation of soluble carbohydrate to insoluble starch in the plastid, intermediate products are formed. In the absence of definite knowledge of the chemical constitution of such compounds it is quite commonly assumed that we are dealing here with a reversible reaction and that clues to the "Aufbau" of starch will be found in the products of its hydrolysis.

Mikosch (1885) called attention to a zone surrounding the young starch grain in the leucoplast which he believed was the "mother substance" from which new starch was formed. Salter (1898) also described such an area, which he interprets as a zone of starch of greater density than that of rest of the grain.

Denniston (1905) observed a distinct orange-staining layer around growing starch grains of *Canna* stained in Flemming's triple stain. He regards this layer as being composed of a transitional material. He observes that a new layer of starch first appears as a narrow violet-stained crescent in the midst of the orange zone. This isolated violet zone gradually widens in the direction of the latest formed layer of starch until the enclosed part of the orange zone is completely replaced with violet-staining starch. The latest part of the layer to be deposited is pale violet as contrasted with the deep violet first-formed part of the lamella. Denniston suggests that the formation of the new layer may be due to the condensation of carbohydrate material from smaller carbohydrate-like molecules, brought about by the abstraction of water, or other similar chemical change. The suggestion is also made that the orange zone is already a carbohydrate material which is later transformed into starch. The latter suggestion is regarded as being the most probable.

Although not attempting to explain the cause of stratification, Denniston regards the phenomenon as being due to the layers of varying densities in the starch grain. Those layers retaining the most stain are regarded as the most dense on the assumption that the stain is removed with less difficulty from the less dense layers.

The material for this study was fixed in weak chrom-acetic mixture, in Benda's fixative and in Merkel's fixative, the time being from 24 to 48 hours. The cotyledons of the young seeds were used in all cases. When very small, the entire cotyledon was fixed, after dissecting it out of the

seed coat. Larger cotyledons were cut into small pieces before fixation. In the case of the very youngest cotyledons, portions of the entire pod were fixed. Portions of living cotyledons were also used with vital stains and with the iodine test and Fehling's reaction.

Most of the sections were stained with Flemming's triple stain. With this stain the nucleoli and certain bodies, probably protein in nature, stain red; the body of the plastids stains deep orange, the cytoplasm a distinctly paler orange and the starch grains violet. Not all the structures that stain violet are necessarily starch, but any substances within the plastid retaining the violet stain is quite obviously starch. This has been proved conclusively by tests made with iodine and with the polariscope. With Heidenhain's iron haematoxylin, with the fixatives used, the cytoplasm stains gray, the plastids blackish and the starch remains unstained.

The so-called vital stains, methylene blue, neutral red and Janus green, were used in an attempt to determine the nature and the origin of the leucoplasts. Other sections were treated with a modified Millon's solution (the Sachs test for dextrin) with the hope of obtaining some light on the composition of the vacuolate centers of the smaller plastids.

In the living cells of very young cotyledons there are minute spherical bodies in the cytoplasm adjacent to the cell membrane. With neutral red solution (1-500) the bodies stain a dark red in contrast with the paler red of the cytoplasm. In these same cells slightly larger bodies have the appearance of being hollow, showing a dark red peripheral region and light central areas, with the neutral red. This appearance is probably to be interpreted as showing a dense protoplasmic shell surrounding either a watery protoplasmic center or a non-protoplasmic vacuole. With Janus green and methylene blue the smaller bodies stain respectively green and blue, and the larger ones show respectively green and blue borders with light centers.

When tested with iodine, the lighter vacuole-like centers of the bodies in question show no positive color reaction. The iodine test also gives negative results with cells which have been treated with a chloral hydrate solution in order to swell any starch inclusions in the central area. Examination of this central region with the polariscope shows no figures characteristic of starch. Thus the above results indicate that there is no starch in these central regions at this stage in the development of these bodies.

With Fehling's solution the lighter central areas show a light brick red color which disappears upon being placed in absolute alcohol. The old Sachs test for dextrin was a brick red color reaction with Fehling's solution which was not removed with absolute alcohol. This test has been

discredited (Zimmerman, 1893) since pure dextrin cannot reduce Fehling's solution.

A brick red color with Fehling's solution, even though not permanent, is very significant and indicates that an incipient reduction of the copper has taken place due, no doubt, to the presence of some aldehyde carbohydrate.

In the fixed and sectioned material of these youngest cotyledons, the cytoplasm of the peripheral layer contains minute rounded bodies which lie right at the limit of clear vision, probably  $\frac{1}{4}$  micron or less. These are stained orange in Flemming's triple stain (fig. 2a). These orange-staining bodies occupy the same position in the cell, are similar in size to those bodies which stain red with neutral red in unfixed material. They are undoubtedly identical with them. Other bodies slightly larger,  $\frac{1}{2}$  micron in diameter, in fixed material, show minutely granular, orange-stained peripheral layers with paler central regions that contain no starch and show no traces of granularity (fig. 2b). These are comparable in size and general appearance to the bodies showing thick dark red borders and light centers when stained with neutral red in fresh material. This pale orange central area is the same as the central region which reacts light brick red with Fehling's solution in the slightly larger bodies of the fresh cells.

The cells of the fresh cotyledons a few days older than those referred to above contain, in addition to the previously discussed rounded bodies, others noticeably larger. These bodies when stained with neutral red show dark red peripheries and have the lighter centers somewhat larger than those already described. These appear homogeneous throughout, but when tested with iodine there is to be seen in its central part a definitely marked area which gives the characteristic reaction for starch. Around this minute blue-stained starch grain there is a zone of the central area which shows no reaction for starch. These larger bodies with small starch grains in their lighter central areas are very similar to those smaller ones, the central areas of which show no starch. The central portion of the larger bodies is, however, often eccentric so that the orange-staining peripheral regions are thicker at one end.

In fixed material of the same age, these earliest starch grains retain none of the violet of Flemming's triple stain (fig. 3a). With the polariscope they show the figures characteristic of starch. With Flemming's triple stain considerable care must be taken to keep the violet dye in the large grains even, so it is not surprising that in these very smallest grains the stain is lost.

It seems clear that the deep orange-staining zones surrounding the

small starch grains are to be regarded as leucoplasts. These are similar to and occupy the same position with relation to the central areas as those of the smaller bodies with central zones containing no starch. It may therefore be concluded that the latter are also plastids. These can be traced back through an unbroken series to those small bodies which lack the lighter central zone and which are therefore also plastids or primordia of plastids (fig. 4b). These smaller plastids are very minute and numerous in the young cells and it is impossible to make any definite statement as to their origin. In no case, however, were they observed to be dividing, so that the assumption that they arise *de novo* from the cytoplasm seems justified.

In sections from older cotyledons, stained with Flemming's triple stain, the stages in the development of the starch grain may be observed. As has already been made clear, there appears in the smaller, deep orange-staining plastids, a central area of a texture and staining reaction different from the periphery (fig. 5a) which shows no indication of starch with the polariscope. Slightly larger plastids (fig. 5b-g) show very minute crosses with the polariscope; they do not occupy the whole of the central area. In the centers of still larger plastids these small starch grains now stain readily with the crystal violet and they do not fill entirely this central area but are surrounded by a zone staining light orange (fig. 5h). The starch grain thus develops in the midst of this material which gives the temporary reaction with Fehling's solution.

In the formation of a second layer of starch around this first minute grain there is deposited around it a paler violet-staining layer (fig. 5i). The orange-staining layer between the plastid and the starch grain tends to maintain its original thickness although, according to Denniston's observations on *Canna*, it is very probable that a part of it is utilized in the formation of the new layer. In a few cases, in the larger starch grains, a dark layer surrounds a paler center (fig. 6a). It may be that these are transverse sections of elongated starch grains cut near the end, since none of the smaller ones were seen with light central layers surrounded by a darker layer.

The growing starch grain (fig. 6c) is composed of distinct, alternating layers of dark and light violet-staining material with a light orange-staining layer, similar to that designated by Denniston (1905) as the transitional zone lying between the starch grain and the plastid material. There is no gradual transition from the light staining starch to the darker staining in each lamella as in the starch grain of *Canna* and other similar starch grains. The number of layers is not as great as in the *Canna* or potato starch grain, usually not exceeding five or six.

In the bean starch grain new layers are formed at the outer extremity



of the latest formed old layer of the starch grain. In case the latest formed layer stains pale violet, there arises at its outer extremity a layer staining distinctly darker (fig. 6b-c). This layer widens gradually and when it has grown to the average thickness there is formed around it another layer staining pale violet. Thus the new layers are growing into the orange-staining zone from the latest formed layer of starch. It seems obvious that with actively growing starch grains there is an area within the plastid which is not starch but which has a chemical composition intermediate between the soluble carbohydrates and starch.

With the older starch grains the deep orange-staining plastids which surround them are often thicker at one end so as to form a cap-like structure (fig. 6b-c). In such starch grains the developing layer of starch arises earliest on that end of the grain where the cap-like part of the leucoplast is found and gradually grows around the grain forming a layer approximately uniform in thickness.

Some of the starch grains which are apparently not growing do not have the light orange zone so that the starch is in direct contact with the granular plastid (fig. 6d). It seems reasonable to assume that these plastids are temporarily inactive.

#### DISCUSSION

It cannot be said that the question of the origin of plastids in the vascular plants has ever been fully settled. Schimper's view of the continuity of the plastid through the life cycle of the plant, while somewhat discredited in the vascular plants, has not been disproved beyond all possibility of doubt. On the other hand the origin of the plastid *de novo*, from undifferentiated cytoplasm has not been finally proved. Recently Miss Stone (1932) has presented evidence of the presence of chlorophyll in undifferentiated cytoplasm of cells of young leaves of potato and condensation of this chlorophyll-bearing cytoplasm to form chloroplasts is described. It seems surprising that such obvious condensations of cytoplasm to form chloroplasts as Miss Stone describes could have been overlooked so long. Her account of this phenomenon will undoubtedly stimulate new work in this phase of plastid formation. More recently Kiyohara (1935) has described plastids in the eggs and pollen tubes of certain angiosperms and is of the opinion that his findings present positive proof of Schimper's view.

In *Phaseolus vulgaris* undoubted leucoplasts containing very small starch grains may be traced through an unbroken series to minute structures which are obviously also plastids. Since these are very small and very numerous it is impossible to determine their origin, but there is no evi-

dence of their having arisen from similar bodies by division. Although the exact origin has not been determined, the most reasonable conclusion seems to be that they have arisen *de novo* from the cytoplasm. It seems very probable that plastids may be formed in a different manner in the different plant groups and in different phases in the life cycle of the same group. For example, multiplication by fission is easily followed throughout the period of growth of many algae, while in the higher plants it is difficult to find stages of plastid fission except in fully developed chloroplasts.

As has already been observed by Mikosch (1885) and Salter (1898), the very young plastid becomes differentiated into a peripheral layer and a central vacuole-like layer previous to the beginning of starch formation. In *Phaseolus* the peripheral layer is noticeably granular and stains quite strongly with orange G. The layer is regarded as the active or protoplasmic part of the leucoplast. The central region is homogeneous and lacking in granularity and, in *Phaseolus*, stains faintly with orange G. Although this central area differs from the peripheral layer in texture and refractivity, as well as staining reaction, it is not impossible that it is protoplasmic and may be regarded as a part of the leucoplast which either is being transformed or is engaged in transforming some carbohydrate into starch.

The color reaction of the central area of the leucoplast with Fehling's solution is of considerable significance and points to the presence of an appreciable amount of an aldehyde carbohydrate. That the reaction is not permanent may indicate that glucose or other actively reducing carbohydrate is not present. The appearance of the young starch grain, following so closely upon the appearance of this vacuolar stage, suggests very strongly that polysaccharide molecules of considerable size are present in this central area.

The difference between the deposition of starch in *Phaseolus vulgaris* and in *Canna* is of considerable interest. In the former, new layers are apparently formed by a transformation of that part of the orange-staining zone adjacent to the latest formed old layer of the starch grain and growth is away from the center. On the other hand, according to Denniston (1905), new layers in the *Canna* starch grain appear first as crescent-shaped masses in the midst of the thick part of the eccentric orange-staining zone, and gradually extended toward the last formed layer until it is reached. The layers in the starch grains in *Phaseolus* stain alternately dark and light with iodine or gentian violet, with no gradual transition of the one into the other. In *Canna* there is a gradual transition in each layer from dark violet on the outside to light violet on the inside of the layer.

Starch grains of certain other plants, as some of the cereal grains, show no lamellae at all. Zwickler (1921) has attempted to demonstrate that the

presence or absence of lamellae is correlated with an excess or deficiency of certain electrolytes. Wheat starch, showing no distinct lamellae, normally contains an excess of calcium ions, while potato starch with its conspicuous lamellae contains an excess of potassium ions.

This work of Zwikker is but one of many on the chemistry of the starch grain from a colloid-chemical view point. From Samec's (1927) exhaustive review of the subject it will be seen that it is one of great complexity. No substantial agreement has been reached as to the relation of the carbohydrate starch to the mineral constituents of the starch grain. The data accumulated, however, point clearly to a relationship between such elements as phosphorus, silicon, potassium and calcium and the characteristic reaction of different starch grains to malt extract and other hydrolytic agents, the formation of colloidal pastes and probably the characteristics of their lamella formation. The difference in the lamellation in the starch grains of *Phaseolus* and *Canna* may very well be connected with characteristic differences in the mineral content of the grains.

The starch grain is clearly not a simple structure made up of the carbohydrate starch with the mineral constituents adhering in an indefinite manner to its exterior, but a close association exists between these two types of components. The mineral compounds may lie between the micellae which make up the composite starch crystal or may even be in loose chemical combination with them.

#### SUMMARY

1. Very young leucoplasts contain vacuole-like central areas which do not react as starch but which show a distinct brown-red color reaction with Fehling's solution, which color is removed by absolute alcohol. This reaction must indicate the presence of an aldehyde carbohydrate.
2. The young starch grains originate in the vacuole-like central areas of these plastids.
3. Surrounding the growing starch grain there is a persistent zone having similar color reactions to the vacuole-like area.
4. New layers of starch are formed at the outer extremity of the last formed old starch grain and grow outward.

This work was completed at the botanical laboratories of the University of Texas. The writer wishes to express her sincere appreciation to Professor Frederick McAllister for his assistance and criticisms.

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#### Explanation of plate 1

All drawings were made with the aid of a camera lucida the magnification being 1750 times.

Fig. 1. Portion of a cell from a very young cotyledon stained with Heidenhain's iron haematoxylin showing the minute plastids (a) and the slightly larger plastids (b) with vacuole-like centers containing no starch.

Fig. 2. Portion of a cell from a very young cotyledon stained in Flemming's triple stain showing minute orange-stained plastids (a) and slightly larger orange-stained plastids with vacuole-like centers containing no starch.

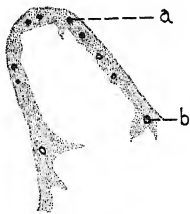
Fig. 3. Portion of a cell from a cotyledon a few days older, stained with Flemming's triple stain, showing in addition to the smaller plastids, those which contain small starch grains which have not retained the violet of the stain.

Fig. 4. Entire cell from an older cotyledon stained with Heidenhain's stain, showing various stages in the development of the plastids—the larger ones containing small starch grains.

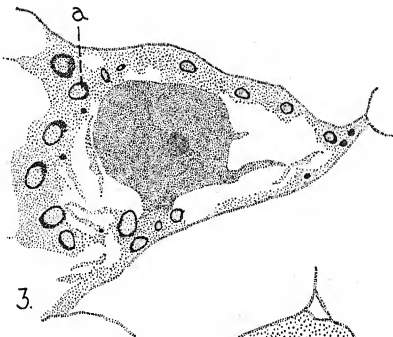
Fig. 5. Successive stages in the development of young starch grains, from an old cotyledon, stained with Flemming's triple stain.

- a. Small plastid with vacuole-like center containing no starch.
- b-g. Plastids containing small starch grains that do not retain the violet stain.
- h. Plastid showing violet-staining young starch grain surrounded by the light orange zone.
- i. Plastid showing a young, dark violet starch grain with a pale violet layer surrounded by a pale orange zone.

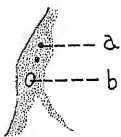
Fig. 6. Entire cell from an old cotyledon showing starch grains in various stages of development. Stained with Flemming's stain.



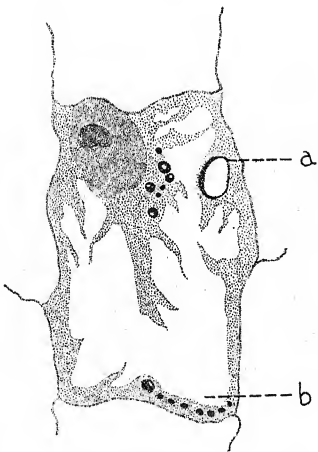
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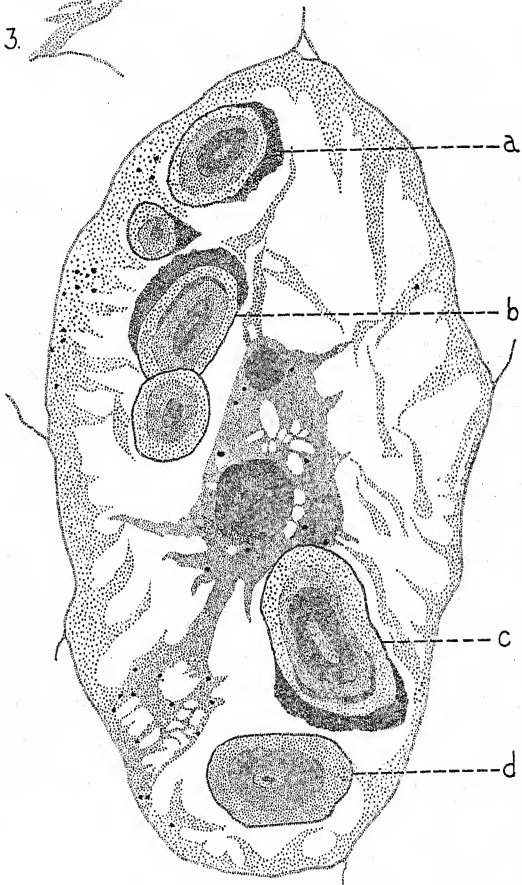
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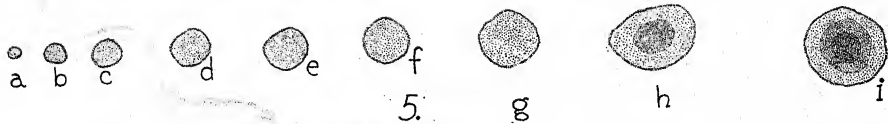
2.



4.



6.



5.



## The development of the embryo of *Zizania aquatica* in the seed and in artificial culture

CARL D. LARUE AND GEORGE S. AVERY, JR.

(WITH EIGHT FIGURES)

The normal embryogeny of certain grasses is well known: *Avena fatua* L. (Cannon, 1900), *Poa annua* L. (Souèges, 1924) and *Zea mays* L. (Randolph, 1936). The embryos of these three species, upon their development into seedlings are representative of two of the three morphological types distinguished by Van Tieghem (1897). It has been shown since that they are all fundamentally one type, appearing differently upon development because of the difference in location of the meristematic region in the first internode (Avery, 1930). If the species indicated above may be considered typical of the family, the general course of embryogeny is the same for the approximately 5000 species (Bews, 1929) of grasses. In the structural aspects of its development into a seedling *Zizania* follows closely that of *Avena*.

Although the culture of plant embryos *in vitro* has been demonstrated many times (Hannig, 1904; Dietrich, 1924; Tukey, 1934; etc.), the culture of embryos starting with relatively young stages is of recent date; apparently no comparative studies have been made of embryogeny *in vivo* and *in vitro*.

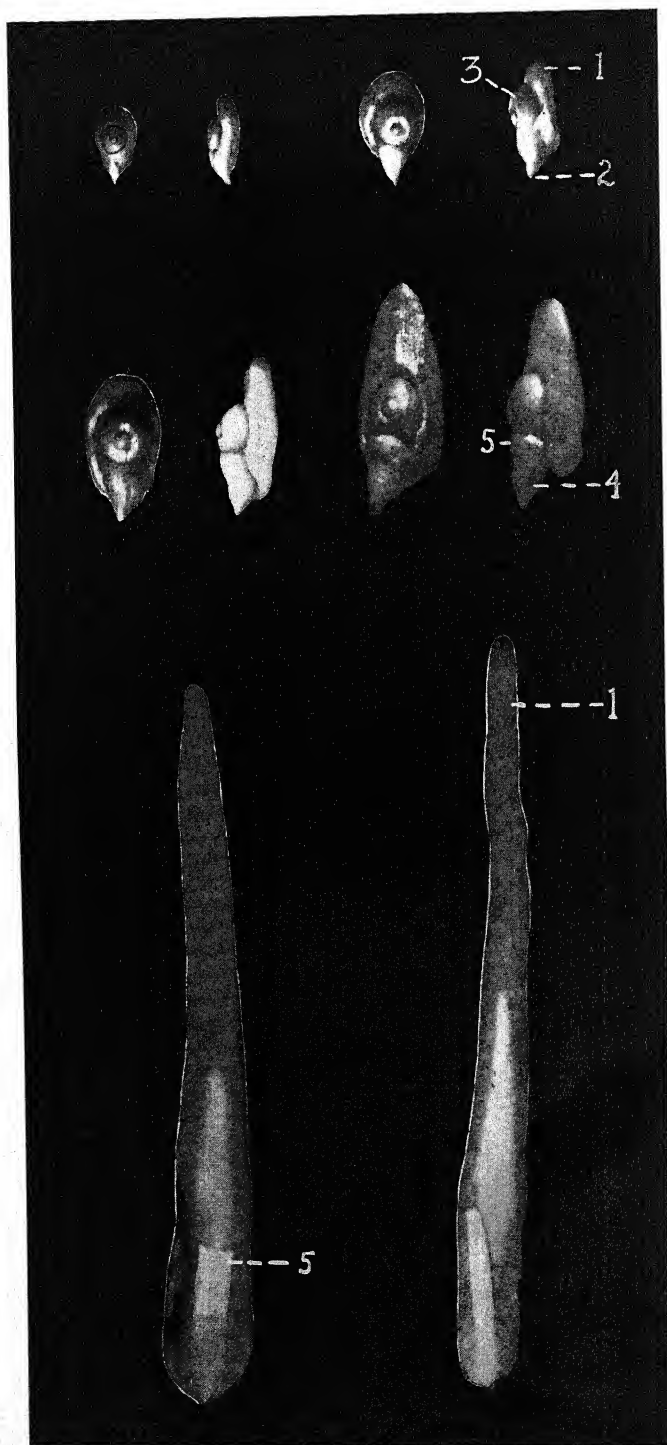
It has been pointed out (LaRue, 1936) that in maize the cotyledon ceases to grow when the embryos are cultured on agar. The question at once arises as to whether embryos in culture continue to develop as "normal" embryos, or, whether their normal growth and form is dependent upon their presence within the tissues of the parent plant.

The embryo of *Zizania* was chosen for this study because it possesses (1) a cotyledon which changes in the course of its development from a flat circular disc to a markedly linear organ. In the course of this development its width increases only five times, but its length 125 times, i.e., in normal embryogeny it shows marked polarized growth. It possesses (2) an epiblast which undergoes changes similar to those of the cotyledon but lesser in degree. Such changes in the length-width ratio of these two structures are so pronounced that any departure from normal embryogeny may be detected.

Is the growth and form of the cotyledon (and epiblast) inherent in the genotype, or is its development subject to environmental circumstances?

### MATERIALS AND METHODS

Embryos were removed from ovaries by dissection under a low-power





binocular microscope. They ranged in stage of development from the smallest which could be removed readily (0.2 mm. in diameter) to fully grown embryos. Aside from the sterilization of all dissecting instruments, etc., no further sterilization was attempted; little difficulty was encountered in removing the embryos aseptically, and placing them on agar media in Petri dishes.

The culture medium used was made up with the salts of White's (1934) solution, two per cent cane sugar and one per cent agar-agar. The yeast extract of White's solution which had been found unnecessary for the growth of maize embryos (LaRue, 1936), was omitted.

For studies on normal embryogeny the embryos were dissected from their ovaries at different stages of development, fixed in formalin acetic alcohol or Nawashin's solution, imbedded in paraffin, etc. The artificially cultured embryos were grown for 5 days in diffuse light or in the dark under ordinary laboratory conditions. They were then fixed and imbedded by the same procedure as that used for the normal embryos; all were cut at a thickness of 6-10 microns and stained with fast green.

The 5-day period for the growth of the embryos was chosen because in that interval of time mature embryos reached the stage at which the shoot burst through the coleoptile thus marking the beginning of their development as seedling plants. The smaller the embryo (upon transfer to agar culture) the longer the time required for it to reach this stage. All but the smallest embryos were grown ultimately to the stage of rupture of the coleoptile, but the significant changes in their development were initiated, at least, within the 5-day period.

#### OBSERVATIONS

*Gross development of normal embryos and embryos in culture.* Since our aim was a study of comparative embryogeny *in vivo* and *in vitro*, no attempt was made to start with embryos smaller than could be removed readily (0.2 mm.). A study of the early phases of embryogeny *in vitro* awaits improved techniques; early development seemed less important to this study because the early stages are concerned more with increase in number of cells than with differentiation. We chose to study the period of development in which the embryo acquires its most characteristic features.

In order to determine the relative ages of the embryos used in this study, their normal embryogeny (in the developing seed) was studied in relation to time (table 1).

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Fig. 1. Embryos of *Zizania aquatica*: 0.2mm., 0.3mm., 0.7mm., 0.9mm., 5mm., and 12mm. (under varying magnifications). 1, cotyledon; 2, suspensor; 3, coleoptile; 4, coleorhiza; 5, epiblast.

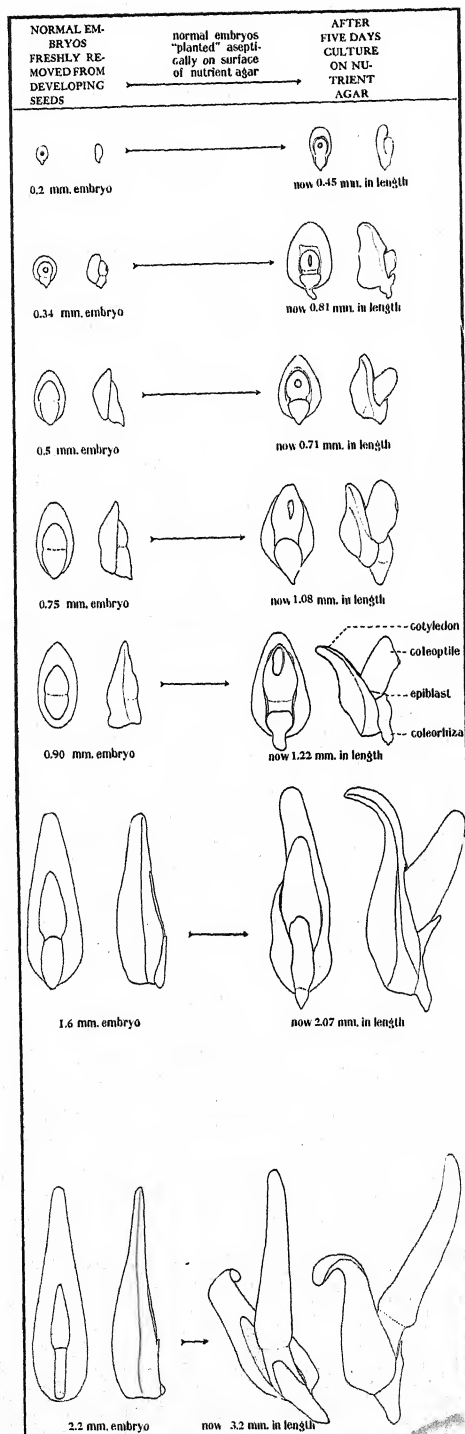


TABLE 1  
Data on growth in length of embryos of  
*Zizania*

DAYS AFTER POLLINATION	LENGTH OF EMBRYOS IN MM.
3	0.1
5	0.15
7	0.35
9	1.0
11	1.5
13	2.25
15	4.0
17	8.0
19	10.0

Upon removal to agar culture, the embryos of all but the smallest sizes grew readily. The mature (embryos 10–12 mm. in length) but "unripe" seeds required no rest period; when planted they would germinate at once. When once "ripened," however, the seeds would not germinate even if the pericarps were cut open, although the embryos if removed and placed on nutrient agar, grew satisfactorily.

A comparison of growth rate in normal embryogeny and cultured embryos is not possible. Total length-growth of an embryo in the seed is much greater than when in culture and presumably the increase in volume is of the same degree. An embryo

Fig. 2. *Zizania aquatica*; diagrams of normal embryos as removed from ovaries, and of similar embryos after 5 days culture on nutrient agar. Note the development of the coleoptile (and of the coleorhiza in the larger embryos) during the period of growth in culture.

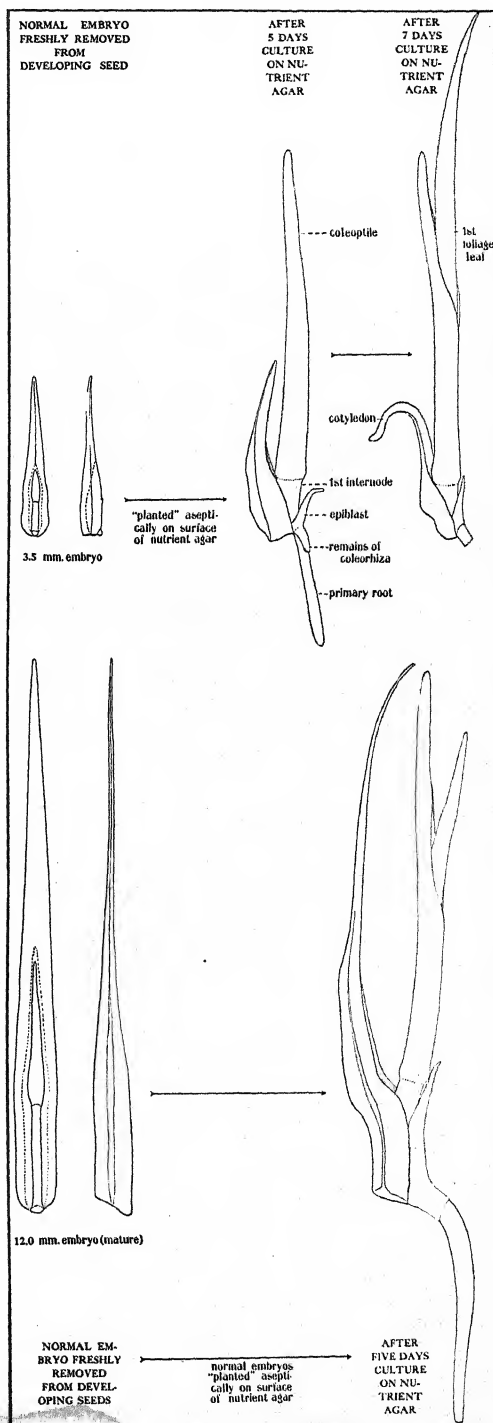
2.2 mm. long (about 13 days after pollination) became 3.2 mm. long after 5 days in culture. If left undisturbed in the seed for this length of time, the same embryo would have increased to 8 mm. in length. But such a comparison obscures the facts; length-growth of the cultured embryos means growth of the coleoptile and first internode, while that of the normal embryo represents increase in length of the cotyledon.

The major differences between the two sets of embryos are differences in form. See figures 1 to 3 for illustrations of this development.

#### MICROSCOPIC OBSERVATIONS ON THE DEVELOPMENT OF THE NORMAL EMBRYOS AND EMBRYOS IN CULTURE

Embryos 0.2 to 0.35 mm. (figs. 1 and 2) upon removal from ovaries often double their length after 5 days in culture, but undergo no further differentiation. The stem growing point, upper portion of the coleoptile, and the cotyledon are clearly dis-

Fig. 3. *Zizania aquatica*; continuation of fig. 2. The coleoptile, first internode, and primary root have elongated markedly after 5 days in culture; the cotyledon and the epiblast do not show further development.



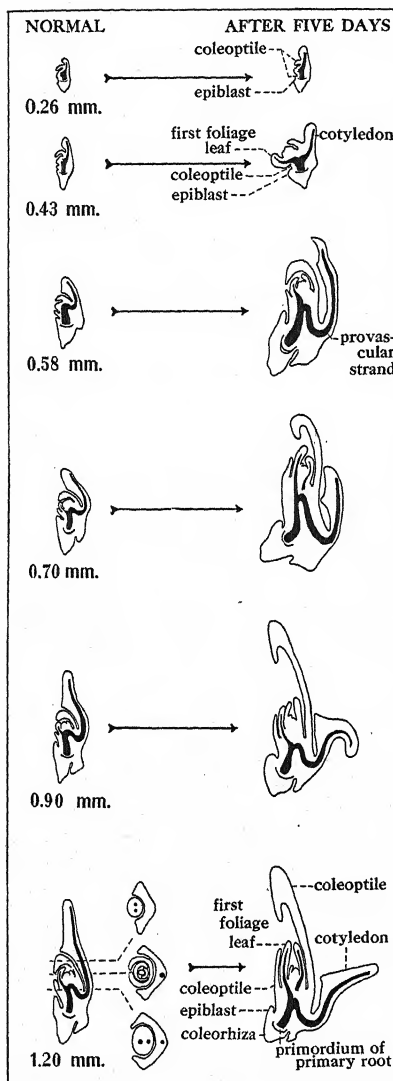


Fig. 4. *Zizania aquatica*; diagrams of median longsections of normal embryos of various sizes, and of similar embryos after 5 days culture on nutrient agar.

tinguishable (figs. 4 and 6); the provascular strand is barely discernible in the latter. The root primordium, not yet differentiated in normal embryos of this size, fails to differentiate during the five days in culture.

Normal embryos 0.4 mm. or more in length at the time of transfer to agar, underwent the following structural changes in the course of five days in culture (figs. 4, 5 and 7): (1) The cotyledon and epiblast underwent a slight increase in size, but there was no evidence of cell division continuing in these structures after the transfer of the embryos to agar culture.

(2) The coleoptile in 0.4 to 0.7 mm. embryos increased in size as a result of the enlargement of its cells, but there was no evidence of a continuation of cell division; however, cell division in this structure continued in culture if the embryos were 0.9 mm. or longer at the time of transfer. The "pore" in the more or less conical coleoptile seldom closed in the embryos which were 1.5 mm. or less in length at the time of transfer to agar.

(3) Either the first foliage leaf or the first internode were the initial structures to undergo marked development when the embryos were transferred to agar; in either structure, there was a long period of cell division after the transfer.

(4) The primary root, although clearly differentiated, is the last structure to undergo discernible change after transfer of the embryos to culture. Its growth is slow in embryos less than about 3.0 mm. in length at the time of transfer.

## DISCUSSION

It is clear that when embryos of *Zizania* were placed on nutrient agar, the cotyledon and epiblast ceased to grow; in contrast, the shoot primordium (and in older embryos, the primary root) departed from its slow growth and differentiation, and began what was virtually a precocious "germination" or development into the seedling stage (similar to the gross morphological development of maize embryos in culture, (LaRue, 1936). *Zizania* is an excellent subject for the study of comparative embryogeny *in vivo* and *in vitro* because the mature normal embryo possesses a cotyledon which extends the entire length of the fruit, often extending around the end of the caryopsis and downward on the back side; the epiblast also is unusually long and prominent. In embryos transferred to agar culture both these organs fail to continue their polarized growth. It is obvious that the continued elongation of these organs is a matter of embryonic development conditioned by factors present in the growing ovary. No investigation has been made to determine the nature of these factors, but whatever they may be, we know that normal embryogeny is absolutely dependent upon them. Removed

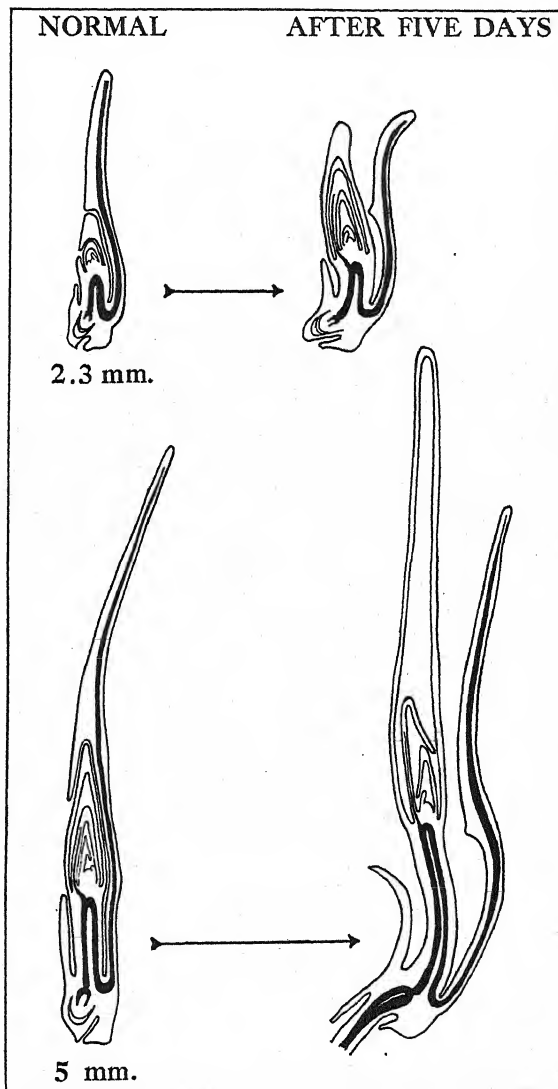


Fig. 5. *Zizania aquatica*; continuation of Fig. 4.

that normal embryogeny is absolutely dependent upon them. Removed

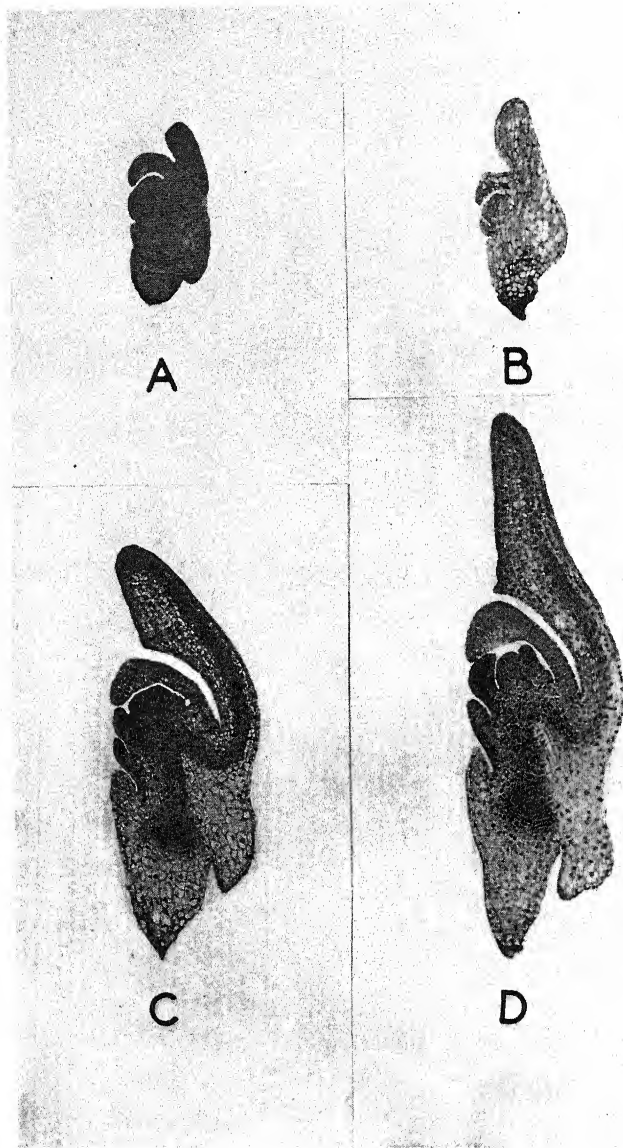


Fig. 6. *Zizania aquatica*; A, C, and D, photomicrographs of median longisections of normal embryos; A, 0.26 mm.; B, same, after 5 days in culture, now 0.43 mm.; C, 0.70 mm.; and D, 0.90 mm.

from their influence the embryo rapidly becomes a seedling, i.e., its axial development begins. The comparative study of embryos *in vivo* and *in vitro* offers a method of investigating the analysis of the factors which control normal embryogeny.

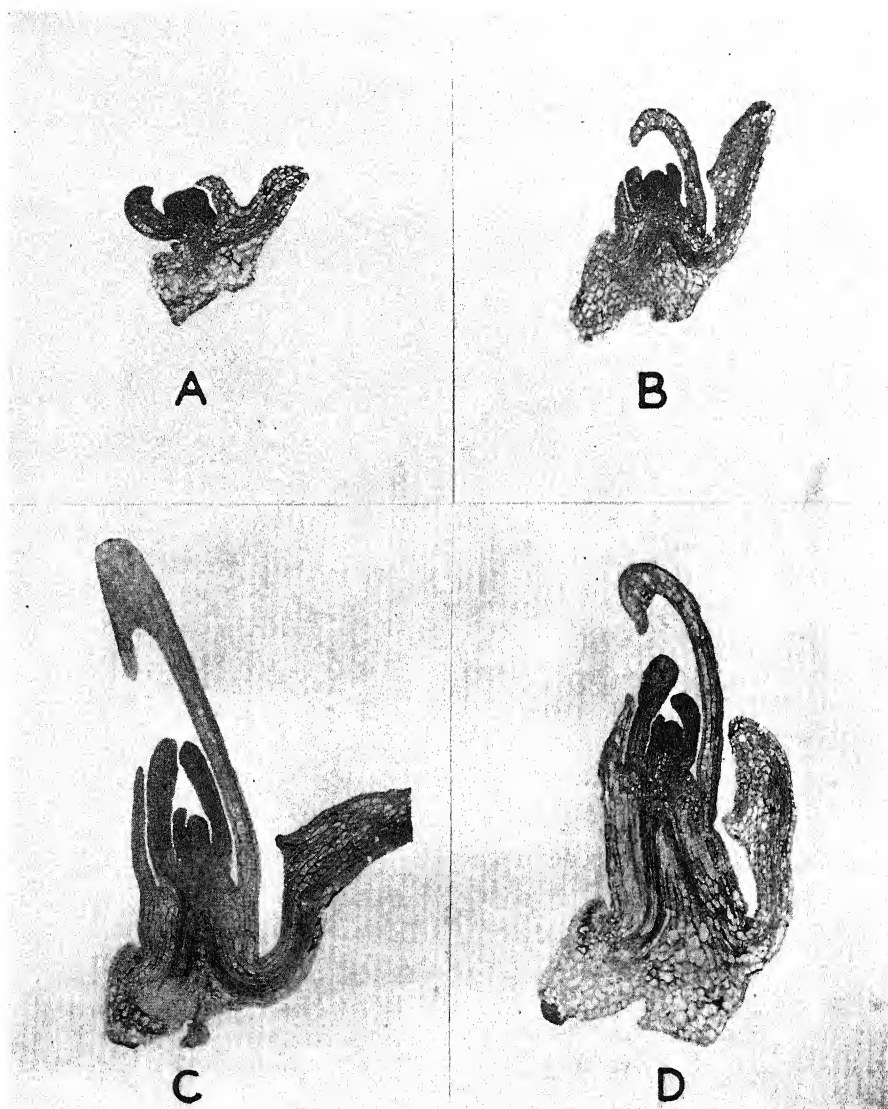


Fig. 7. *Zizania aquatica*; photomicrographs of median longisections of embryos of various sizes after 5 days culture on nutrient agar. Compare with fig. 4 for sizes of these embryos at time of removal from ovaries.

#### SUMMARY

1. The embryo of *Zizania aquatica* was chosen for this study because the marked elongation of the cotyledon and the epiblast during embryogeny *in vivo* provide a means of determining departures from the normal during development *in vitro*.

2. Embryos of different ages were dissected from their ovaries. Representative sizes were fixed, imbedded, sectioned and stained, and a corresponding set of embryos was placed on nutrient agar in Petri dishes. After 5 days in culture the embryos of this second group were sectioned for comparison with the normal embryos.

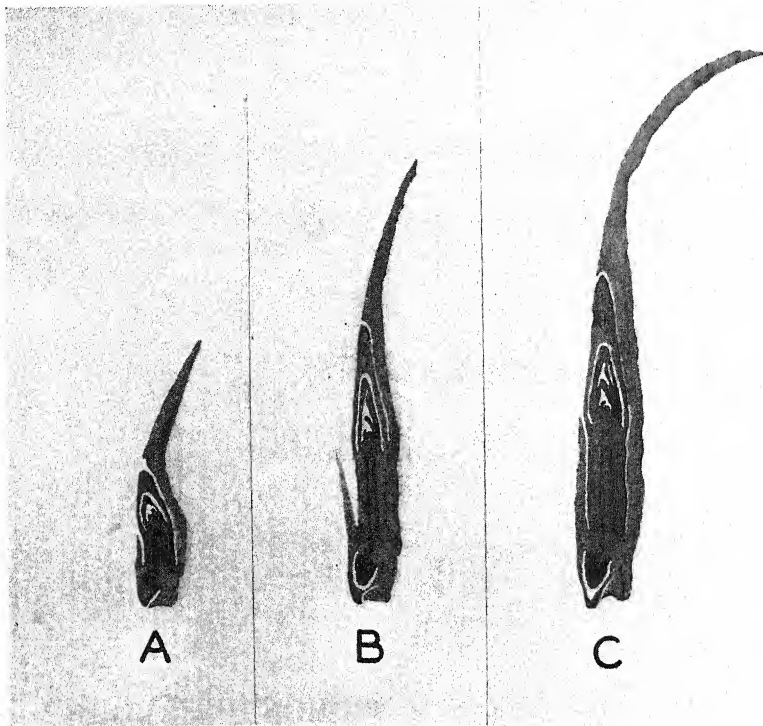


Fig. 8. *Zizania aquatica*; photomicrographs of longisections of normal embryos of different sizes. A, 2.3 mm.; B, 3.8 mm.; C, 5.2 mm. See fig. 5 for diagrams of A and C. Longisections of mature embryos differ in no important respect from C, except that the cotyledon usually attains a length of approximately 12 mm. See fig. 3.

3. Embryos of all but the smallest sizes were grown to the seedling stage in culture. Small embryos took a somewhat longer time to reach the seedling stage. Embryos smaller than 0.4 mm. failed to reach the seedling stage.

4. Determinations were made of the time required after pollination for the development of the different sizes of embryos, in the course of normal embryogeny.

5. The normal development of embryos has been traced and compared with that of those grown *in vitro*. Growth in culture is generally character-



ized by *precocious* development of the shoot and retarded growth of the primary root. In older embryos elongation of the primary root is not appreciably retarded. Growth of the cotyledon and epiblast is arrested upon transfer to agar culture. Normal growth and development of the embryo is dependent upon its presence within the tissues of the parent plant.

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<sup>1</sup> A part of this work was done while both authors were in residence at the University of Michigan Biological Station (no. 640 in the series of botanical papers from the Univ. of Mich.). All photomicrographs by Donald D. Irish, The Dow Chemical Company, Midland, Michigan.



## A new green alga: *Oedocladium Lewisii*

L. A. WHITFORD

(WITH PLATE 2)

Although *Oedocladium protonema* has not been collected since the genus was established by Stahl, five additional species have been described. The writer was fortunate enough to collect a seventh in autumn, 1936. For several weeks it was widely distributed but not abundant in lower piedmont North Carolina; and in December it was collected in the extreme eastern part of the State. Like most of the species it is terrestrial and is always associated with *Vaucheria*, *Botrydium*, liverworts, and mosses. It forms tiny colonies on very moist sandy or loam soil, that was plowed the current year. Half shaded areas in bottom-land fields are the most likely collecting places. To the naked eye it resembles moss protonema but is slightly yellowish green and grows in scattered tufts one to two millimeters in diameter. Rainy or cloudy and cool weather for several weeks is probably necessary for it to become abundant enough to be readily collected.

### *Oedocladium Lewisii* sp. nov.

Monoica; oogoniis singulis, plerumque terminalibus, globosis, operculo inferior. Oosporis globosis, membrana triplici, omne levi vel mesosporio angulato (in sectione optica undulato), oogonium complentibus. Cellulis suffulcio sine pigmentum, saepe moribundus. Antheridiis ad 9-cellularibus, gametis masculis singulis. Cellulis vegetativis subcylindricis, cellula terminali apice conica. Cellulis vegetativis superterraneis  $13-22\mu \times 60-106\mu$ . cell. veg. subterraneis  $4-11\mu \times$  ad  $257\mu$ . Oogonis  $45-70\mu$  diam. Oosporis  $42-60\mu$ . diam. Antheridiis  $16-21\mu$  latis,  $12-21\mu$  longis.

Herb. L. A. W. 550-554.

Monoecious; oogonium solitary, nearly always terminal, operculum inferior. Oospore globose with a triple membrane, the middle layer smooth or angulate (undulate in optical section) the other layers smooth, nearly or entirely filling the oogonium. Suffultory cell without color usually empty. Antheridia up to 9; sperm single. Vegetative cells subcylindric, terminal cells with conic apex,  $13-22\mu \times 60-106\mu$ . Rhizoidal cells  $4-11\mu \times$  (up to)  $257\mu$ . Oogonium  $45-70\mu \times 48-70\mu$ . Oospore  $42-60\mu$  in diameter. Antheridium  $16-21\mu \times 12-21\mu$ .

The species was collected in October and November at five stations in Wake County, North Carolina, and once each in Durham and Harnett counties. In late December it was also collected in Craven, Carteret, and Pamlico counties in the coastal plain.

There is a superficial resemblance to *O. Hazenii*, but the inferior operculum and empty suffultory cells readily separate it from all known species.

It is the second described species with an operculum and the other character seems to be unique for the genus. In the last division of the suffultory cell, all of the chlorophyll and most of the cytoplasm migrates into the forming oogonium. A nucleus and a small amount of much vacuolated cytoplasm remains in the suffultory cell. By the time the oospore is mature this protoplasm has usually disintegrated leaving a dead cell supporting the oogonium.

Observation of living, dividing cells and studies of preserved material by simple microchemical methods, lead the writer to believe that cell division occurs according to the theory of Kraskovitz for *Oedogonium*. That is, when the ring forms in a dividing cell, it forms not as an isolated mass of new cell wall material laid down at that particular point, but is merely an inward bulging portion of a new wall layer laid down, and completely covering the inside of the mother cell (figs. 6, 8). The mother cell ruptures under the inward bulging portion (ring) and this stretches or extends itself to form the wall of the daughter cell. The cross wall is not a "floating" structure but forms *in situ* at the point of attachment, and after the nucleus and cytoplasm have migrated into the daughter cell. Branches are formed by the failure of the mother cell to rupture all the way around. In this case the ring bulges out through the slit formed on the side of the mother cell and forms the first cell of the new branch. Aberrant L-shaped cells sometimes observed, are good proof that branches form in this way (fig. 7). Rhizoidal or semi-rhizoidal cells continue to grow by intussusception near the tip of the cell. In this case most of the protoplasm, and chlorophyll if present, is concentrated in the distal end, leaving the other end of the cell colorless and vacuolate.

A more complete description of cell formation in *Oedocladium* will be published later

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#### Explanation of plate 2

All drawings made with the aid of a camera lucida. Cells in figures 6, 7, and 8 swollen with 60-65% sulfuric acid.

Fig. 1. Young plant showing growth habit.

Fig. 2. Oogonium formation showing migration of chloroplast into the oogonium.

Fig. 3. Oogonium with colorless suffultory cell.

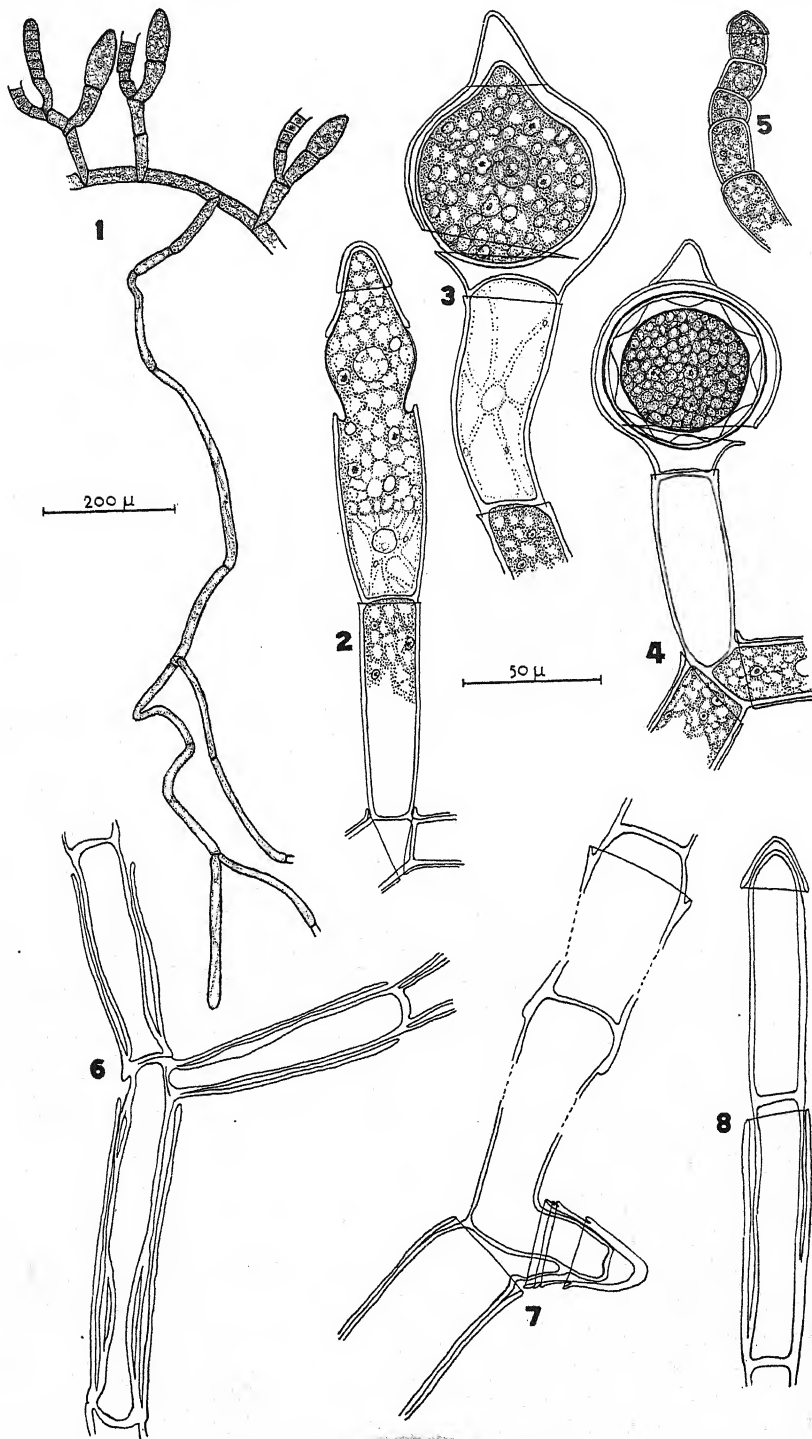
Fig. 4. Oogonium with mature oospore and empty suffultory cell.

Fig. 5. Antheridia.

Fig. 6. Cells swollen with strong sulfuric acid showing that after cell division has occurred cell walls have two or more complete layers.

Fig. 7. L-shaped cell resulting from incomplete rupture of mother cell wall.

Fig. 8. Showing that cell wall consists of one layer before division and of two layers after a cell has divided.



WHITFORD: OEDOCLADIUM

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## Delphinium carolinianum and its allies

ROBERT F. MARTIN

Few genera of North American plants are more puzzling than the delphiniums. Among the entities differences in flower color, leaf segmentation, pubescence, and habit are often unaccompanied by tangible structural changes, and determination depends upon the weighing of several evasive and independently varying characters. The roots and seeds are reliable enough but they are, in general, essentially alike among closely allied species. Furthermore, a great deal of herbarium material lacks these organs.

No group is responsible for more confusion than the *Delphinium carolinianum* complex. The present notes result from examining a series of sheets preparatory to attempting a monograph of the genus in North America.

The first recognizable species of the group was described by Walter<sup>1</sup> as *D. carolinianum*. Michaux<sup>2</sup> redescribed this species as *D. azureum*, a name commonly encountered in literature and on herbarium labels. Dr. Blake<sup>3</sup> has pointed out that Walter's specimen is only a fragment and not determinable. I believe, however, it is safe to assume on the basis of distribution that Walter collected the species that has been accredited to him. More species have been added from time to time by Nuttall, D. Don, Huth, Greene, and Rydberg. Lately Miss Perry<sup>4</sup> has contributed a variety. Most confusion exists in the application of Huth's, Greene's, and Rydberg's names.

In my opinion, use of the orientation of the spur, its degree of curvature, and the distance of the bracteoles from the receptacle to distinguish entities is unjustified. Throughout the genus the upper part of the pedicel and the receptacle are bent in anthesis so that the flower is horizontal or turned downward. Later by unequal growth in the pedicel, it is moved through 90° or 180° to an erect position, and this same growth causes the bracteoles to become remote.

Unless otherwise indicated, all specimens cited are in the United States National Herbarium. Those in the herbarium of the National Arboretum are followed by N. A. Those specimens found in both collections are followed by U. S., N. A.

<sup>1</sup> Walter, T., *Flora Caroliniana* p. 155. 1788.

<sup>2</sup> Michaux, A., *Fl. Bor. Amer.* 1: 314. 1803.

<sup>3</sup> Blake, S. F., *Rhodora* 17: 130. 1915.

<sup>4</sup> Perry, L. M., *Rhodora* 39: 20-22. 1937.

- a. Seeds wing-margined
  - Pubescence glandular, at least in part. 1. *D. carolinianum* (typical).
  - Pubescence not glandular. 1a. *D. carolinianum*, var. *crispum*.
- aa. Seeds squamellate, not wing-margined. b.
  - b. Flowers white, greenish or yellowish white, or blue tinged.
    - Pubescence glandular, at least in part. 2. *D. virescens* (typical).
    - Pubescence not glandular. 2b. *D. virescens* var. *camporum*.
  - bb. Flowers blue. 2a. *D. virescens*, var. *vimineum*.

1. *D. CAROLINIANUM* Walt. Fl. Car. 155. 1788. *D. azureum* Michx., Fl. Bor. Am. 1: 314. 1803; *D. Nortonianum* Mack. & Bush, Trans. Acad. Sci. St. Louis 12: 82. 1902; *D. azureum*, var. *Nortonianum* Palmer & Steyermark, Ann. Mo. Bot. Gard. 22: 543. 1935; *D. carolinianum*, var. *Nortonianum* Perry, Rhodora 39: 20. 1937.

I am unable to distinguish *D. Nortonianum* from large, deep blue states of *D. carolinianum*. In all its characters, size and color excepted, it seems identical.

Georgia to Texas and Missouri. Also from Florida to Virginia, according to Small.

GEORGIA: Bibb Co., Biltmore Herb (3767c); ALABAMA: Lee Co., Pollard & Maxon 15; MISSISSIPPI: Hinds Co., Cook, May 24, 1925; TEXAS: Walker Co., Dixon 555; Woods Co., Reverchon 4341; OKLAHOMA: Lefflore Co., Blakeley 1419; ARKANSAS: Nevada Co., Hollister 12; MISSOURI: Jackson Co., Bush 377, isotype of *D. Nortonianum*.

1a. *D. CAROLINIANUM*, var. *CRISPUM* Perry, Rhodora 39: 21. 1937.

In addition to the absence of glandular hairs, the carpels seem longer than in typical *D. carolinianum*. The specimen of Patterson here cited has mature seeds quite like those of the species.

Alabama to Arkansas, north to Missouri and Illinois.

ALABAMA: Perry Co., Smith, 187(6?); ARKANSAS: Carroll Co., Palmer 5585; MISSOURI: Barry Co., Bush 228; ILLINOIS: Henderson Co., Patterson, no date given.

2. *D. VIRESCENS* Nutt. Gen. N. Am. Pl. 2: 14. 1818: *D. azureum*  $\beta$  *virescens* Huth, Helios 10: 34. 1892: *D. Penardi* Huth, loc. cit: *D. albescens* Rydb, Bull. Torrey Cl. 26: 583. 1899: *D. carolinianum*, var. *Penhardii* A. Nels. in Coult. & Nels. New Man. Rocky Mtn. Bot. 193. 1909: *D. virescens*, var. *Penardi* Perry, Rhodora 39: 21. 1937.

This is the common species of the prairies and plains, and ranges into the foothills of the Rockies. Huth's *D. Penardi*, I am unable to distinguish. Attempts have been made to separate it as the form with the upper part of the stem eglandular. It appears, however, that the glandular hairs may be present on any or all parts of the stem indiscriminately.

Louisiana and Texas, north to Colorado and Wisconsin.



LOUISIANA: Jeff Davis Parish, *Palmer* 7672; TEXAS: Brazos Co., *Palmer* 9369; Victoria Co., *Tracy* 9243; OKLAHOMA: Woods Co., *Stevens* 551; KANSAS: Riley Co., *Norton* (Kans. St. Ag. Col. 8); NEBRASKA: Grant Co., *Marsh*, June 25, 1916, (N. A., U. S.); SOUTH DAKOTA: Moody Co., *Ball* 875; MINNESOTA: Hennepin Co., *Mearns* 270; IOWA: Harrison Co., *Eggleston* 15135; COLORADO: Arapahoe Co., *Eggleston* 11216, (N. A., U. S.)

- 2a. *D. virescens*, var. *vimineum* (D. Don), comb. nov.: *D. vimineum* D. Don in Sweet Brit. Flow. Gard. Ser. 2, pl. 374. 1838: *D. azureum*, var. *vimineum* A. Gray, Bot. Gaz. 12: 52. 1887: *D. macroseratilis* Rydb. Bull. Torrey Club 26: 585. 1899.

Because of its rugose-squamellate seeds this form belongs here rather than with *D. carolinianum*, which it resembles in habit.

TEXAS: Harris Co., *Palmer* 9620; Kerr Co., *Heller* 1723;

- 2b. *D. virescens*, var. *camporum* (Greene), comb. nov.: *D. camporum* Greene Erythea 2: 183. 1894: *D. Wootoni* Rydb., Bull. Torrey Club 26: 587. 1899.

Doctor Greene's name has been considered a synonym of *D. Penardi* Huth and specimens of this variety are generally determined as *D. Penardi*. It is clear, however, from Green's description and from plants determined by him that he described the eglandular plant of the Mexican border states. Huth's plant from his description was glandular and therefore, as I see it, the same as typical *D. virescens*. Var. *camporum* may be distinguished by the subscapose stem and often by the blue tinged flowers.

Texas to Arizona.

TEXAS: Bexar Co., *Havard*, March 1882; Terrell Co., *Palmer* 33546; NEW MEXICO: Dona Ana Co., *Wooton*, May 26, 1905; ARIZONA: Co-chise Co., *Eggleston* 19863.

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## The cultural characteristics of the species of *Fomes*<sup>1,2</sup>

W. A. CAMPBELL

Within the past several years, the identification of the causal organisms of timber decay has become of considerable importance especially in connection with improvement cuttings in second-growth hardwood timber. Some investigators have been puzzled by the multiplicity of fungous forms which may be isolated from decayed wood and have felt that the positive identification of these fungi is a hopeless task. This study has been undertaken in order to work out a practical system whereby fungi from decayed wood may be identified and to study the cultural characteristics of the species of a single genus. The genus *Fomes* was selected because a number of isolates of the different species were already available and, since the sporophores are perennial, additional isolates could be obtained at any time.

### REVIEW OF THE LITERATURE

Since Hartig's discovery of the relation between the mycelium of a fungus present in wood and the condition of decay which existed, many investigators have demonstrated that this mycelium, when isolated under aseptie conditions, could be made to grow upon artificial media in test tube and Petri dish cultures.

The following investigators have pointed out that cultural characteristics are valuable means for the identification of the organisms of decay: White (1910) first cultured a member of the genus *Fomes*, using *Fomes applanatus*, and made observations on cultural characteristics; Baxter (1924) pointed out the possibility of using growth rate to separate fungi closely related in form and demonstrated the production of two kinds of secondary spores in culture by *F. fraxineus*; Mounce (1929) made extensive observations on the cultural characteristics of *Fomes pinicola* using malt agar as a standard medium. The most complete study of cultural characteristics was made by Long and Harsch (1918) who tested a number of wood destroying fungi including ten species of *Fomes*. They were particularly interested in the development of sporophores in culture. They originated a number of descriptive terms which have been used in the

<sup>1</sup> Submitted in partial fulfillment of the requirements for the degree of Doctor of Philosophy in the Department of Botany, The Pennsylvania State College, State College, Pa., August, 1935.

<sup>2</sup> The writer is particularly indebted to Dr. L. O. Overholts, of the Department of Botany, The Pennsylvania State College, for his suggestion of the problem and for his encouragement and aid during the course of the experimentation and during the preparation of this article.

present study. Fritz (1923) demonstrated beyond a doubt that individual species of wood-destroyers produced very characteristic mats in culture and that these characteristic mats were constant for a given species. Snell, Hutchinson and Newton (1928) demonstrated that closely related forms could be separated by growth rate at constant temperatures. Sluzalis (1933) worked out the cultural characteristics of a number of fungi, paying particular attention to the formation of secondary spores. Within the last few years Cartwright (1929, 1934), Verral (1934) and Baxter (1932) have made more or less extensive studies of wood-destroyers, including many species of *Fomes*, in culture, demonstrating the practicability of making identifications of sporophores and rots on the basis of cultural characteristics.

#### MATERIALS AND METHODS

The purpose of this study has been to work out a suitable system for the identification of *Fomes* species in culture, based upon as simple a procedure as possible. With this in mind, the fungi to be identified were grown on a single kind of agar, for a limited period, in Petri dishes at room temperature. Identification was then based upon macroscopic and microscopic characters. To this basic procedure has been added (1) growth at constant temperatures and (2) reactions obtained with tannic and gallic acid media. At all times, however, emphasis has been placed upon the development of a simple, practical technique which may serve as the basis for future studies on the cultural characteristics of other fungi.

*Media.* Since personal observations and the experience of others indicate that nothing of great importance is to be gained by growing a fungus on a variety of agars, malt agar, which has been recognized for some time as the standard medium for culturing wood-destroying fungi, was chosen as the medium to be used in this study. Other agars, when used, were merely for the sake of providing supplementary data. The malt agar was prepared by dissolving 20 grams of agar in 1 liter of distilled water either in the autoclave or over an open flame. When the agar was dissolved, 15 grams of Difco malt extract was added and the resulting solution poured into 500 cc. flasks and sterilized for 20 minutes at 15 pounds pressure. The weight of materials and time of sterilization were carefully checked in order to make each batch comparable.

No attempts were made to adjust the pH of the malt agar. Test samples taken at various times indicated a range of from 5.2 to 5.8. Since wood-destroying fungi prefer a slightly acid medium and since the pH may vary within rather wide limits for these fungi, the control of pH within these narrow limits was not considered important.

Tannic and gallic acid media used to differentiate between brown-rot fungi and white-rot fungi were prepared according to Bavendamm's (1928) suggestion, in total concentrations of 0.5 per cent. Since it is impossible to sterilize malt agar containing tannic and gallic acid, the malt agar was prepared as given above using instead of 1000 cc. of water, 800 cc. The proper amounts of the tannic or gallic acids were dissolved in 200 cc. water and sterilized. While still hot the two were mixed together and poured into Petri dishes. When only a few plates of tannic acid medium or gallic acid medium were needed, the malt agar was poured into the dishes and a small amount of the acid dropped in with a scalpel. This short method gave results comparable to more accurate methods since the concentrations of the tannic and gallic acids may vary considerably without affecting results.

No attempt was made to accurately measure the amount of agar used in Petri dish cultures. A thick layer, however, was poured into each dish, considerably in excess of the amount actually required by the fungus, in order to make sure that moisture content would not be reduced appreciably in the 14 days that the dishes were in use.

For stock cultures, 18 mm. test tubes were used. These tubes were filled with 15 cc. of agar and given a comparatively short slant in order to reduce the surface exposed to air. For subcultures a longer slant was used, as here the object was to secure a surface from which inoculating material might be taken rather than to prevent drying of the agar.

*Treatment of cultures.* The stock cultures were kept in racks in a cupboard where they received but weak diffused light. These cultures were renewed every four months.

Whenever inoculations of Petri dishes were to be made, subcultures were started from 2 to 3 weeks in advance. These subcultures were usually made in Petri dishes although long-slanted test tubes were also used.

In order to secure the most constant results, the following procedure was adopted. Material for the inoculum was taken from near the outer margin of the mats, care being taken to include some of the superficial hyphae as well as the submerged hyphae, the size of the piece being maintained as constant as possible, about 3 mm. square. This was placed with the mycelium side down upon the agar and gently patted in order to bring it into close contact. All transfers were made in a small room with doors and windows closed. No precautions were observed other than mopping up thoroughly with mercuric chloride just prior to transferring, and confining transfer work to the early hours before any sweeping or general moving about of people had stirred up the dust. Very few contaminations resulted and these were never serious enough to interfere with the work.

Cultures to be grown at room temperature were left on the desk in the same room used for transfer work. This room was on the southwest side of the building and had one window. The distance from the window varied from 10 to 12 feet. The shades were adjusted to provide diffused light at all times, although no attempt was made to keep the amount of light constant. Cultures grown at constant temperatures were kept in complete darkness.

In order to eliminate variable results at higher temperatures when working with constant temperature ovens, cultures to be incubated at 36° C were kept at room temperature for 48 hours prior to being placed in the oven, those at 31°, 24 hours, those at 21° and 26° were placed there directly after inoculating. At the higher temperatures it was felt advisable to allow the mycelium to make some growth into the agar before being placed under, in many cases, adverse temperatures for growth and development.

*Recording data.* Data as to rate of growth, appearance of mat, color, and microscopic features were taken from Petri dish cultures at intervals of seven and fourteen days. Records for test tube cultures were taken at one, two, four and eight weeks. Observations as to macroscopic and microscopic features were taken at least three different times, corresponding to different seasons of the year for each species, and the final description is a composite of the separate descriptions. Colors are described in terms of Ridgway's Color Manual.

Photographs of Petri dish cultures were made at intervals of seven days for fast growing species and at fourteen days for slower growing species. These photographs are designed to show the more usual characteristics of the cultures rather than exceptions.

In all cases emphasis is laid upon the fact that the final descriptions are the result of numerous observations made over a period of 18 months. In this way it has been possible to observe variations of individual cultures under conditions that are bound to vary from season to season.

*Source of cultures.* Most of the cultures used were isolates obtained from sporophore tissue. Some isolates from the rotted wood were also used. Most of these cultures were available from Dr. L. O. Overholts' collection at The Pennsylvania State College; additional ones were secured from Mr. R. W. Davidson, Office of Forest Pathology, Washington, D. C.; Dr. Irene Mounce, Central Experimental Farm, Ottawa, Canada; Dr. J. S. Boyce, Osborn Botanical Laboratory, New Haven, Conn.; Dr. W. H. Snell, Brown University, Providence, R. I. Other collectors have supplied smaller numbers of cultures and additional ones were obtained from time to time by trips into the field. In most cases identification of the sporo-

phores from which cultures were made has been checked by Dr. Overholts.

In all, 31 species of *Fomes* are reported on in this investigation. This includes the several varieties of *F. igniarius* and the one variety of *F. robustus*, as well as the sterile fungus tentatively designated as the *Sterile Fomes*. One hundred and seventy-nine separate isolations of the *Fomes* species have been examined, distributed as follows among the different species: *F. annosus*, 4; *F. applanatus*, 12; *F. Calkinsii*, 4; *F. conchatus*, 5; *F. densus*, 4; *F. Everhartii*, 11; *F. fomentarius*, 12; *F. fraxineus*, 2; *F. fraxinophilus*, 12; *F. fulvus*, 2; *F. geotropus*, 2; *F. igniarius*, 12; *F. igniarius* var. *laevigatus*, 8; *F. igniarius* var. *populinus*, 4; *F. juniperinus*, 1; *F. lobatus*, 3; *F. marmoratus*, 3; *F. meliae*, 2; *F. officinalis*, 4; *F. ohienensis*, 1; *F. Pini*, 7; *F. pinicola*, 18; *F. rimosus*, 11; *F. robustus*, 8; *F. robustus* var. *tsugina*, 4; *F. roseus*, 5; *F. scutellatus*, 5; *F. subroseus*, 9; *F. tenuis*, 2; *F. torulosus*, 2; *Sterile Fomes*, 1. Of the species listed above, to my knowledge, the following have not been cultured previously or at least accounts of their cultural characteristics have not appeared in the literature: *F. Calkinsii*; *F. conchatus*; *F. densus*; *F. geotropus*; *F. juniperinus*; *F. lobatus*; *F. marmoratus*; *F. meliae*; *F. ohienensis*; *F. robustus*; *F. scutellatus*; *F. tenuis*; *F. torulosus* and the *Sterile Fomes*.

#### DESCRIPTION OF CULTURES

In the descriptions of cultures an attempt has been made to include all variations that may be expected within a given species when grown on malt agar, at room temperature, in diffused light. Where a number of isolations were available for any species, this desideratum is at least approximated. Where only one or two isolations were available, the description can apply only to these isolations and may or may not be characteristic of the species as a whole. The phrase, *Type Culture*, is used to indicate an isolate which exhibits all the diagnostic characteristics of the species in question, and is a valid culture to be used for purposes of comparison. In case other investigators are interested in these *Type Cultures*, transfers of the same will be maintained at The Pennsylvania State College and have been sent to the Division of Forest Pathology, Washington, D. C.

Growth at seven days and fourteen days is expressed as the diameter of the colony in centimeters. The figures given indicate the range which may be expected from cultures grown in diffused light at room temperature. If a culture grew 6 to 7 cm. in seven days its growth has been described as *rapid*; if from 5 to 6 cm., *moderately rapid*; from 3 to 4 cm., *slow*; and from 1 to 3 cm., *very slow*.

Records of growth at constant temperatures are expressed as average colony diameters for cultures kept in total darkness. It is not feasible to

compare growth rates for cultures kept in dark with those maintained in light at the same temperature as light may considerably affect growth rate.

Texture of mat is described by the following terms taken for the most part from Long and Harsch's list:

*Appressed*: Mycelium which is prostrate on surface of agar.

*Raised*: Forming a mound on agar as opposed to appressed.

*Cottony*: Erect, rather long mycelium spreading in all directions.

*Downy*: Short, fine hairs loosely scattered over surface of mat giving it a downy appearance.

*Felty*: Matted with intertwined hairs resembling felt.

*Woolly*: A dense mass of mycelium, consisting of long, tortuous, matted hairs.

*Plumose*: Tufts of mycelium with a central axis from which short hyphae radiate.

*Silky*: Long parallel threads of mycelium, more or less prostrate like combed silk

*Nodulose*: Forming definite nodes or bunches.

*Tufted*: Forming tufts.

*Floccose*: Thin, cottony pubescence, collected in very minute tufts.

*Pulverulent*: Having a powdery or dusty appearance.

*Poroid*: Covered with pores.

*Homogeneous*; Having same appearance throughout.

*Mat proper*: Portion of mat in direct contact with agar.

*Central zone*: In case mat is divided into definite areas, the portion about center.

*Marginal zone*: Part of mat surrounding central zone.

*Margin proper*: Region of advancing growth.

*Fimbriate*: Possessing a fringed edge.

*Submerged hyphae*: Hyphae growing in contact with or through agar.

*Superficial hyphae*: Aerial hyphae usually forming surface of mat.

In case it has been necessary to make intermediate distinctions between two of the above terms, for example between floccose and cottony, then the compound word, *floccose-cottony*, was used.

In case of reaction with tannic acid, a *strong* reaction indicates that the diffusion zone formed is dark brown and extends considerably beyond the margin of the colony; *moderately strong*, means that the zone is lighter brown and diffuses to a lesser extent; *medium*, means that the zone is light brown and ordinarily not extending beyond the margins of the mat; *faint*, indicates that the reaction is light brown, sometimes difficult to distinguish from the color of the mat proper, and found only under the older portions of the mat. Usually strong reactions will appear in at least 48 hours, while medium and faint reactions will require from four to fourteen days to manifest themselves. In case the reaction is *negative* no discoloration of the agar occurs.

If no secondary spores occur, no mention of spores will be found in the description. Structures not mentioned in the descriptions should be considered as lacking.



1. *FOMES ANNOSUS* (Fries) Cooke. Type Culture: FP-53378-S. Figures 1-3, 99.

Growth rapid, mat 6-8 cm. in 7 days; typical culture white, loose, floccose-cottony to appressed-cottony, homogeneous, azonate, at times much appressed and compacted about center, decidedly pulverulent; more cottony forms vegetative with few conidia, while appressed forms produce conidia in abundance; margin colorless or faintly white, coarsely fimbriate; condiophores very numerous to rare, borne on aerial hyphae with inflated, subglobose tips, 9-15 $\mu$  diameter, covered with numerous sterigmata; conidia obovoid, 5-8 $\times$ 3.5-6 $\mu$ ; submerged hyphae 3-4 (-8) $\mu$ , with cross-walls but no clamps; aerial hyphae 6-8 $\mu$ , granular with deeply staining contents; growth at constant temperatures, 5.5 cm., 21°; 8.0 cm., 26°; 4.3 cm., 31°; 0 cm., 36°; strong reaction with tannic acid media.

In 14 days mat appressed-floccose-cottony to floccose-cottony, usually azonate, pulverulent about inoculum or over entire surface, white, sometimes slightly cream colored; odor faint to prominent, musty.

*Test tube cultures.* White to cream colored up to 4 weeks, becoming cinnamon drab to drab in 8 weeks, mat fragile, pulverulent, at times forming poroid areas made up of closely interwoven hyaline hyphae, thick-walled, uniformly 2 $\mu$ ; no basidia; globose, ellipsoid to short cylindric or irregular-shaped, terminal chlamydospores with definite hyaline wall, 9-15 $\times$ 6-12 $\mu$ , fairly abundant, intermingled with hyaline hyphae.

*Distinguishing characters.* The production of characteristic conidiophores and conidia separates *Fomes annosus* from all other *Fomes* species reported here.

2. *FOMES APPLANATUS* (Pers.) Gill. Type Cultures: 17182-S, 17184-S. Figures 4-8, 100.

Growth slow, mat 2.5-4 cm. in 7 days, typically appressed, thin, colorless to faintly white or chalky white, downy or pruinose, fragile, usually slightly zonate, central portion often much compacted, pruinose-pulverulent, white, forming a tough crust on agar in contrast to fragile, thin, marginal portion; margin proper appressed, colorless, even; submerged hyphae 2-4(-5) $\mu$ , much branched, with abundant clamps; superficial hyphae 2-3(-4) $\mu$ , either resembling submerged hyphae and bearing numerous irregularly divided, staghorn branches, or thick-walled, hyaline; cuticular bodies abundant to rare in compacted central zone, globose, up to 20 $\mu$ ; growth at constant temperatures 4.1 cm., 21°; 5.0 cm., 26°; 5.5 cm., 31°; 1.0 cm., 36°; moderately strong reaction with tannic acid media.

In 14 days mat 5-8 cm. in diameter, appressed, thin, fragile, colorless

to white, usually slightly zonate, downy to pulverulent or pruinose, with compacted white central zone. Unusual forms at times more compacted and much slower growing, or cottony and growing at a faster rate. Cuticular bodies more abundant; odorless.

*Test tube cultures.* Mat white up to four weeks with numerous yellowish compacted masses of crystalline material common along edge of mat on agar cylinder, tough, at times considerably wrinkled. Deepest colors developed in eight weeks mouse gray and Quaker drab, fruiting body produced in only one instance culture F-496, with few mature basidiospores, truncate, light brown  $6-8 \times 4-5\mu$ . On potato-dextrose producing a much wrinkled and contorted mat.

*Distinguishing characters.* *F. applanatus* is readily recognized by the presence of staghorn branches on superficial mycelium and by the absence of chlamydospores. *F. fraxineus* which produces staghorn branches on

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#### Explanation of figures 1-53

Figs. 1-3. *Fomes annosus*. 1, Conidiophore. 2, Chlamydospores from poroid areas. 3, Hyaline hyphae from poroid areas.

Figs. 4-8. *F. applanatus*. 4, Submerged hypha. 5, Superficial hypha. 6, Staghorn branches. 7, Cuticular cells. 8, Basidiospores.

Figs. 9, 10. *F. Calkinsii*. 9, Submerged hypha. 10, Superficial hypha.

Figs. 11, 12. *F. conchatus*. 11, Submerged hypha. 12, Superficial hypha.

Figs. 13, 14. *F. densus*. 13, Submerged hypha. 14, Superficial hypha.

Figs. 15, 16. *F. Everhartii*. 15, Submerged hypha. 16, Superficial hypha.

Figs. 17-19. *F. fomentarius*. 17, Submerged hyphae. 18, Superficial hyphae. 19, Chlamydospore.

Figs. 20-26. *F. fraxineus*. 20, Submerged hypha. 21, Superficial hypha. 22, Staghorn branches. 23, Large chlamydospores. 24, Small chlamydospores. 25, Basidia. 26, Basidiospores.

Figs. 27-30. *F. fraxinophilus*. 27, Submerged hypha. 28, Superficial hypha. 29, Large chlamydospores. 30, Small chlamydospores.

Figs. 31-35. *F. fulvus*. 31, Submerged hypha. 32, Superficial hypha. 33, Incrusted hypha. 34, Basidia and paraphyses. 35, Basidiospores.

Figs. 36-38. *F. geotropus*. 36, Submerged hyphae. 37, Incrusted hypha, 38, Basidia and basidiospores.

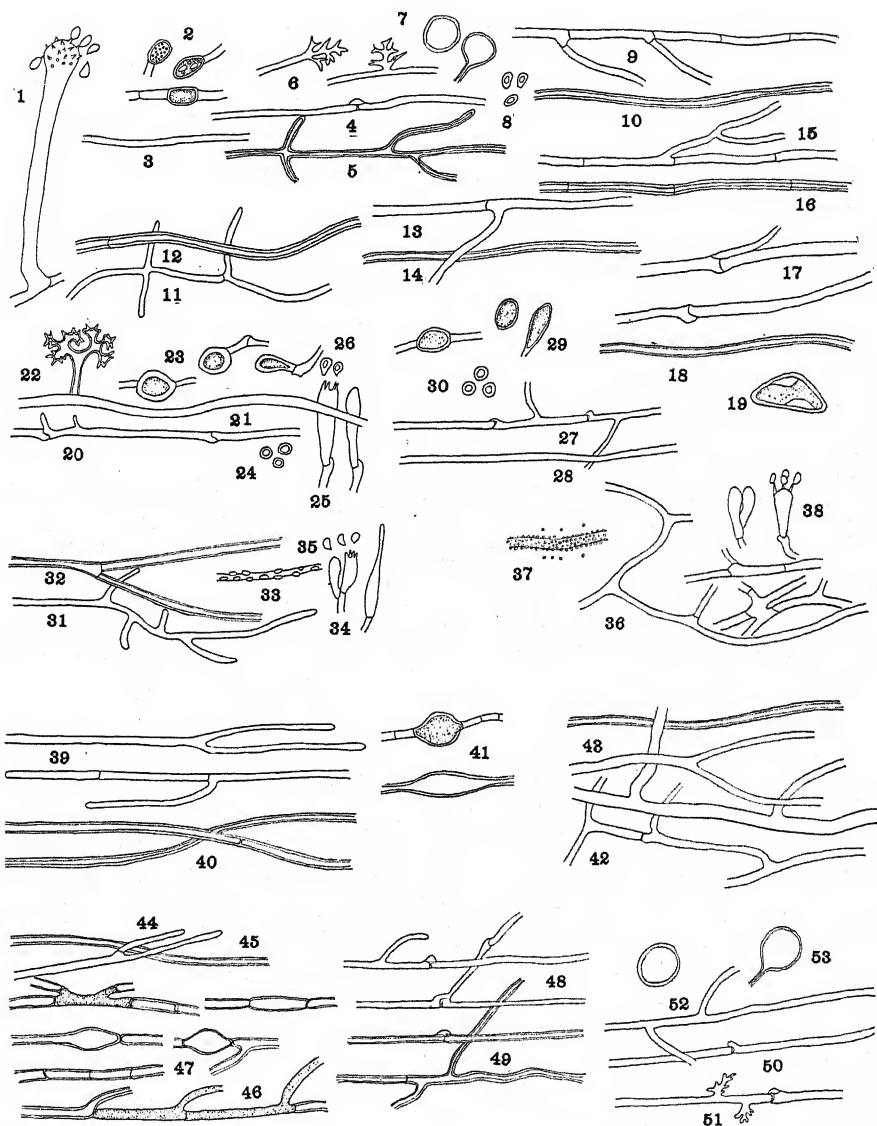
Figs. 39-41. *F. igniarius*. 39, Submerged hyphae. 40, Superficial hyphae. 41, Chlamydospore-like bodies and hyphal swellings.

Figs. 42, 43. *F. igniarius* var. *laevigatus*. 42, Submerged hyphae. 43, Superficial hypha.

Figs. 44-47. *Fomes igniarius* var. *populinus*. 44, Submerged hypha. 45, Superficial hypha. 46, Submerged hyphae broken up into short cells. 47, Hyphal swellings.

Figs. 48, 49. *F. juniperinus*. 48, Submerged hyphae. 49, Superficial hyphae.

Figs. 50-53. *F. lobatus*. 50, Submerged hyphae. 51, Staghorn branches. 52, Superficial hypha. 53, Cuticular cells.



Figs. 1-53. (See opposite page for legend)

superficial mycelium produces chlamydospores in abundance. *F. applanatus* cannot be separated with certainty in every instance from *F. lobatus*. However, the latter species usually has a pronounced compacted yellowish to drab central zone and a loose-cottony or only slightly compacted marginal zone.

3. *FOMES CALKINSII* (Murrill) Sacc. & D. Sacc. Type Culture: 14667-S. Figures 9, 10, 101.

Growth slow, mat 2-3 cm. in 7 days, white at margin, pale orange yellow or occasionally deepening to antimony yellow over central portion, raised, compacted, woolly to felty, often with faint narrow zones; margin white, short cottony, even; submerged hyphae 2-5(-6) $\mu$ . with cross-walls but no clamps, hyphae under colored portion of mat thin-walled, brownish with abundant cross-walls spaced at short intervals; superficial hyphae 2-3(-4) $\mu$ , thick walled, brown, with few cross walls, little branched; growth at constant temperatures 2.0 cm., 21°; 2.5 cm., 26°; 2.5 cm., 31°; trace, 36°; strong reaction with tannic acid medium.

In fourteen days mat 4-5 cm., white at margin to pale orange yellow and antimony yellow over central portion, raised, compacted, woolly to felty, spongy; margin white short cottony, even; odorless.

*Test tube cultures.* Mat in four weeks forming definite fruiting pad on slant, tough, heavy, from mustard yellow, through antimony yellow to yellow ochre and buckthorn brown.

*Distinguishing characters.* *F. Calkinsii* is difficult to separate from *F. robustus* but the former is more delicate, lighter colored and grows somewhat slower, and becomes more pallid in the dark. *F. Calkinsii* is inhibited entirely at 36° C while *F. densus* is able to make good growth. Similarly *F. Calkinsii* may be separated from *F. conchatus*, *F. Everhartii*, *F. rimosus* and *F. torulosus* on temperature relations.

4. *FOMES CONCHATUS* (Pers.) Gill. Type culture: 524 Mad. Figures 11, 12, 102.

Growth very slow, mat 1-2 cm. in 7 days, white with at times a yellowish tinge about inoculum; thin, cottony to thick, felty-cottony, too small to possess many distinctive features and consisting of a white cottony, relatively undifferentiated mass of hyphae; margin white, cottony, fimbriate; submerged and superficial hyphae not distinct, 2-5 $\mu$ , with cross-walls but no clamps; growth at constant temperatures, 1.7 cm., 21°; 2.3 cm., 26°; trace, 31°; 0 cm., 36°; strong reaction with tannic acid medium.

In fourteen days mat 2.5-4 cm., somewhat variable with few dis-

tinctive features, usually raised, compacted felty-cottony about center to more loosely-cottony at margin, compacted central zone varying in color from fawn to buckthorn brown, often partially obscured by white to yellowish superficial covering; marginal zone chalky white; margin proper white, cottony, fimbriate; colored superficial hyphae uniformly  $2-5\mu$ , thick-walled, non-staining, branched, with abundant cross-walls, yellow color of superficial hyphae diffusing strongly in KOH solution; globose vesicular bodies common in some cultures, rare in others, mostly terminal, up to  $20\mu$  in diameter; odorless.

*Test tube cultures.* In 4 weeks mat forming pad on slant, usually uneven on agar cylinder, varying considerably in color from warm buff to yellow ochre and buckthorn brown.

*Distinguishing characters.* *Fomes conchatus* is one of the slower growing colored species of *Fomes* with a restricted temperature range being almost completely inhibited at  $31^{\circ}$  C. It can be distinguished from *F. Pini* by color and temperature relations and from *F. igniarius* var. *populinus* by more rapid growth and by its chalky white mat in early stages and absence of odor.

##### 5. FOMES DENSUS Lloyd. Type culture: FP-52033-S. Figures 13, 14, 103.

Growth slow, mat in 7 days 2-3 cm., straw yellow at margin, gradually deepening to mustard yellow and primuline yellow over inoculum, raised, loosely felty-cottony to woolly, at times compacted, homogeneous, azonate; margin proper even, colorless; submerged hyphae  $3-5(-7)\mu$ , with few cross-walls and no clamps; superficial hyphae moderately thick-walled, yellowish  $2-4\mu$ ; growth at constant temperatures 2.0 cm.,  $21^{\circ}$ ; 2.6 cm.,  $26^{\circ}$ ; 4.7 cm.,  $31^{\circ}$ ; 2.0 cm.,  $36^{\circ}$ ; strong reaction with tannic acid medium.

In 14 days mat 4.5-6 cm., dense, closely compacted, woolly to felty-cottony, nodulose, raised considerably above agar, homogeneous, straw yellow at margin to mustard yellow and primuline yellow at center, superficial raised portion tough, spongy, separating freely from agar, turning ochraceous buff when touched with KOH, later light brown; odorless.

*Test tube cultures.* In 4 weeks mat raised, compacted, with definite fruiting pad on slant, homogeneous in color and texture, tough antimony yellow and yellow ochre.

*Distinguishing characters.* *F. densus* does not separate readily from *F. robustus* and *F. Calkinsii*. However, it does show a considerably faster growth rate at  $31^{\circ}$  than either of these and the yellow color which rarely deepens to antimony yellow is quite distinctive, since both *F. Calkinsii* and *F. robustus* become yellow ochre or darker in Petri dish cultures in 14

days. Both *F. Calkinsii* and *F. robustus* turn brown when touched with KOH without going through an intermediate ochraceous buff stage.

6. *FOMES EVERHARTII* (Ell. & Gall.) von Schrenk Type culture: 17412-S. Figures 15, 16, 104.

Growth slow, mat 2-3 cm. in 7 days, dark, approximately Sudan brown, fragile, not separating from agar, superficial covering thin to dense, ochraceous buff and antimony yellow at center to pale yellow or white at margin, often with a greenish yellow sheen, silky to silky-cottony, partially to completely obscuring color of mat proper; margin colorless to white, appressed to cottony, fimbriate; submerged hyphae from growing tip 2-4(-6) $\mu$ , thin-walled, staining readily with eosin, few cross-walls and no clamps, from mat proper 2-4(-6) $\mu$ , thick-walled with brownish content and with abundant cross-walls; superficial hyphae, 2-3(-4) $\mu$ , thin to moderately thick-walled, darkening in KOH; growth at constant temperatures 2.0 cm., 21°; 3.2 cm., 26°; 3.6 cm., 31°; 1.5 cm., 36°; strong reaction with tannic acid medium.

In 14 days mat 4-6 cm., mat proper Sudan brown, closely compacted to agar, rather thick; superficial covering antimony yellow or pale yellow at center to white at margin, silky to silky-cottony, partially to completely obscuring color of mat proper; odorless.

*Test tube cultures.* Mat in 4 weeks Dresden brown to mummy brown, thick, clinging to agar, superficial covering silky-cottony, antimony yellow to yellow ochre, becoming faded with age, finally warm buff through cinnamon buff to honey yellow.

*Distinguishing characters.* In general *F. Everhartii* if grown in light can readily be distinguished from *F. igniarius*, *F. rimosus* and *F. densus* by dark mat proper and by silky superficial covering, often with a greenish tint, and usually turning vinaceous when rubbed with KOH.

7. *FOMES FOMENTARIUS* (L.) Gill. Type culture: 17041-S. Figures 17-19, 105.

Growth rapid, mat in 7 days 6-7 cm., white to cream colored or light ochraceous buff and light ochraceous salmon, ochraceous color localized about inoculum or covering entire surface, azonate, homogeneous, closely appressed-cottony to appressed-velvety, forming a distinct, somewhat tough film on agar; margin white or colorless, fimbriate; chlamydospores rare or absent, ellipsoid, ovoid, or irregular, 20-28 $\times$ 12-18 $\mu$ , with thick hyaline wall; submerged hyphae, 3-5 $\mu$ , with abundant clamps; superficial hyphae 2-4 $\mu$ , hyaline or colored, thick-walled, uniform, without clamps; growth at constant temperatures 5.0 cm., 21°; 7.0 cm., 26°; 6.4 cm., 31°; trace 36°; strong reaction with tannic acid medium.

In 14 days mat solidly light ochraceous buff to buckthorn brown or with irregular white or cream colored areas, rarely entire mat white or cream colored, forming tough, thin film on agar, surface appressed-velvety; margin against glass often forming distinct, yellowish papillae which contain crystalline material; odor indistinct, sweetish.

*Test tube cultures.* In 4 weeks mat appressed-velvety, cream colored to buckthorn brown, with numerous yellowish papillae against glass later darkening to cinnamon brown and Dresden brown.

*Distinguishing characters.* *F. fomentarius* can readily be distinguished in culture by the thin, velvety, appressed mat and by lack of pore surfaces and vesicular bodies. The only species that it superficially resembles, *F. marmoratus*, produces conspicuous cuticular or vesicular bodies. The yellowish papillae against the test tube glass is characteristic of *F. fomentarius*.

8. FOMES FRAXINEUS (Bull. ex Fries) Cooke-Type culture: FP-57061-S. Figures 20-26, 106.

Growth moderately rapid, mat 5-6 cm. in 7 days, white, homogeneous, appressed, pulverulent to granular about inoculum to appressed coarse cottony near margin; margin proper faintly white, very coarsely fimbriate; chlamydospores very numerous, mostly globose to lemon-shaped, 10-15  $\mu$  in diameter, when mature with heavy hyaline wall up to 4 $\mu$  thick; occasional cultures exhibit few to many clavate, immature basidia which resemble irregular-shaped chlamydospores; submerged hyphae up to 4 $\mu$ , with abundant clamps; superficial hyphae 2-4 $\mu$ , hyaline, thick-walled, often bearing numerous dichotomously divided staghorn branches from tips and sides; growth at constant temperatures 4.0 cm., 21°; 6.5 cm., 26°; 8.5 cm., 31°; 2.5 cm., 36°; strong reaction with tannic acid medium.

In 14 days mat white, appressed, pulverulent to granular or appressed, coarse cottony, with raised velvety patches and at times with faint to prominent poroid areas, white to faintly vinaceous; chlamydospores of type described at 7 days very numerous, in addition poroid areas contain small, subglobose chlamydospores 6-8 $\times$ 5-6 $\mu$ ; immature basidia common in poroid areas, mature basidia rare, clavate 8-10 $\mu$  diameter; basidiospores ellipsoid 5-7 $\times$ 3-4 $\mu$ ; odorless.

*Test tube cultures.* Mat white with sporophore developing on lower half of slant in 4 weeks, pores deep purplish vinaceous, producing subglobose chlamydospores in great abundance.

*Distinguishing characters.* *F. fraxineus* may be distinguished from *F. fraxinophilus*, which it resembles very closely in appearance, by heavy walled chlamydospores, by the staghorn branches on superficial mycelium,

and by the vinaceous color of the pore surface as produced in tube cultures. It may be distinguished from *F. applanatus* and *F. lobatus* by production of chlamydospores and by the formation of pores in tube cultures.

9. *FOMES FRAXINOPHILUS* (Peck) Sacc. Type culture: 15159-R. Figures 27-30, 107.

Growth moderately rapid, mat 4-5 cm. in 7 days, white, appressed nodulose-cottony to appressed velvety-cottony, often forming poroid areas, tough, peeling readily from agar; marginal zone broad, fragile, colorless, appressed-cottony; margin proper colorless, fimbriate; chlamydospores abundant, globose to clavate or irregular,  $8-14 \times 5-8\mu$ , rather thin-walled; submerged hyphae  $1-4\mu$ , clamps abundant; superficial hyphae  $1-3\mu$ , thick-walled, smooth, little branched; growth at constant temperatures 3.5 cm.,  $21^{\circ}$ ; 6.0 cm.,  $26^{\circ}$ ; 7.0 cm.,  $31^{\circ}$ ; 5.0 cm.,  $36^{\circ}$ ; moderately strong reaction with tannic acid medium.

In 14 days mat white, finely nodulose-cottony to velvety-cottony, often with well developed poroid areas over central zone, azonate, tough, peeling readily from agar; poroid areas often producing abundant globose to subglobose, secondary spores,  $6-8 \times 5-6\mu$ , thick-walled, hyaline, produced on short branches of superficial hyphae; immature basidia also produced in poroid areas, no mature basidiospores noted; odor faint, mushroom-like.

*Test tube cultures.* In 4 weeks producing wood colored pores mostly on upper part of slant, rest of mat white, pores containing numerous small secondary spores.

*Distinguishing characters.* *F. fraxinophilus* may be distinguished from *F. fraxineus* by lack of staghorn branches on superficial mycelium and by wood colored pores. *F. fraxinophilus* may be distinguished from all other *Fomes* having a white mat by the production of pores in tube cultures and by the small, subglobose secondary spores.

10. *FOMES FULVUS* Scop. ex. Gill. Type culture: 16870-S. Figures 31-35, 108.

Growth slow to moderately rapid, mat 3.5-5 cm. in 7 days, thin, appressed long-cottony, strongly to faintly zoned, with superficial mycelium orientated toward center, surface about inoculum sometimes covered with scattered patches of compacted, raised, hardened mycelium, which develop into poroid areas, but in other isolates no evidence of poroid areas, in general ochraceous buff to cinnamon buff with compacted, nodulose patches darkening to buckthorn brown; marginal zone greyish white



coarse-cottony; margin proper colorless, even; no secondary spores; immature basidia abundant in poroid areas; submerged hyphae  $2-6\mu$ , without clamps but with cross-walls, gradually grading into white superficial hyphae with definite hyaline wall, often incrustated with large smooth crystals; brown superficial hyphae  $3-4\mu$ , heavy walled, darkening in KOH; growth at constant temperatures 4.5 cm.,  $21^{\circ}$ ; 5.0 cm.,  $26^{\circ}$ ; 4.5 cm.,  $31^{\circ}$ ; 2.5 cm.,  $36^{\circ}$ ; moderately strong reaction with tannic acid medium.

In 14 days mat 8-9 cm., appearance same as at 7 days, poroid areas more numerous giving nodulose to pulverulent appearance to mat, basic portion ochraceous buff to cinnamon buff, poroid places buckthorn brown or darker; secondary spores none; mature basidia clavate to short cylindric,  $10-15 \times 3.5\mu$ , usually forming definite hymenial layer containing narrow paraphyses extending up to  $20\mu$  and occasionally brown setae; basidiospores ellipsoid to allantoid, slightly flattened on one side,  $3-4 \times 2-3\mu$ ; odorless.

*Test tube cultures.* Mat thin, appressed, with hard appearing surface or more cottony, ochraceous buff to antimony yellow and yellow buff with poroid areas or remaining undifferentiated.

*Distinguishing characters.* *F. fulvus* may be readily identified by production of fruiting structures in culture; when these are lacking, however, growth rate and temperature relations must be relied upon to separate it from other rapid growing *Fomes* species.

11. FOMES GEOTROPUS Cooke. Type cultures: FP-55521-S, FP-55558-S  
Figures 36-38, 109.

Growth very rapid, mat 7 cm. in 4 days, white, closely appressed cottony to loosely cottony, homogeneous, very fragile, azonate, closely adhering to agar; secondary spores none; immature basidia at times numerous, often lacking; submerged hyphae small,  $2-3(-4)\mu$ , without clamps; superficial hyphae up to  $7\mu$ , without clamps, staining deeply with eosin, often incrustated; growth at constant temperatures in 7 days, 9.0 cm.,  $21^{\circ}$ ; 15 cm.,  $26^{\circ}$ ; 15 cm.,  $31^{\circ}$ ; 9 cm.,  $36^{\circ}$ ; faint reaction with tannic acid medium.

In 14 days mat white, either closely appressed, pulverulent, homogeneous, with tendency to form sporophores, or loosely cottony, tufted, without sporophores; mature basidia abundant; basidiospores ellipsoid,  $4-5 \times 3-4\mu$ ; odor faint, mushroom-like.

*Test tube cultures.* In 4 weeks, white, appressed or loosely cottony usually portion on agar producing yellowish areas containing crystalline material.

*Distinguishing characters.* *F. geotropus* may be distinguished from all

other *Fomes* species that produce a white mat in culture on growth rate alone, forming a mat 10–12 cm. in diameter in 7 days at room temperature.

12. *FOMES IGNIARIUS* (L. ex Fries) Gill. Type cultures: 17171-S, 17355-S. Figures 39–41, 110.

Growth slow, mat 2–3 cm. in 7 days, raised, compacted woolly to felty or loosely felty-cottony, at times nodulose or ridged, definitely two-zoned, central zone ochraceous buff, through clay color to buckthorn and Dresden brown, marginal zone narrow to broad, chalky white; margin proper colorless to white, somewhat fimbriate; submerged hyphae 2–5 $\mu$ , without clamps; superficial hyphae of two kinds, either colorless up to 7 $\mu$ , with slightly thickened hyaline wall and deeply staining contents, or colored, with thick hyaline wall, non-staining, 2–4 $\mu$ , with few cross-walls; growth at constant temperatures 3.5 cm., 21°; 4.2 cm., 26°; 3.1 cm., 31°; 1.5 cm., 36°; strong reaction with tannic acid medium.

In 14 days mat 5–6 cm., raised, loosely felty to compacted fine-woolly, two-zoned nature less pronounced, central portion yellow ochre to buckthorn brown and often as dark as Sudan brown and antique brown; color often toned down by whitish to yellowish superficial covering, tough, peeling readily from agar in thick felted sheets leaving whitish film attached to agar; secondary spores questionable, occasional globose to irregular thick-walled chlamydospore-like bodies produced up to 30 $\mu$  in diameter; odorless.

*Test tube cultures.* Fruiting pad formed on agar slant, usually fine woolly, warm buff to ochraceous buff, rest of mat buckthorn brown to Dresden brown, often with alternating light and dark bands on agar cylinder.

*Distinguishing characters.* It is possible to confuse *F. igniarius* with certain other colored species such as *F. robustus*, *F. rimosus*, *F. torulosus* and *F. densus*. However, *F. igniarius* possesses a more distinctly two-zoned nature and peels more readily from the agar leaving a whitish film attached. It differs from *F. igniarius* var. *laevigatus* by growing at a much slower rate and in possessing no odor.

13. *FOMES IGNIARIUS* var. *LAEVIGATUS* Fries. Overh. Type culture: 17359-S. Figures 42, 43, 111.

Growth rapid, mat 4.5–6 cm. in 7 days, usually two-zoned, central zone closely compacted, felty to felty-cottony, moderately thick, homogeneous, peeling evenly and cleanly from underlying agar, ochraceous tawny to buckthorn brown, marginal zone appressed cottony to woolly, changing from white on outer limits to yellowish on inner, adhering to agar, thin; margin proper white, thin, scraggly, coarsely fimbriate; sub-

merged hyphae, 3-7 $\mu$ , cross-walls common, clamps none or rare; superficial hyphae of two kinds, white, staining in eosin, with moderately thick hyaline wall 3-7 $\mu$ , or brown, thick-walled, non-staining, 1.5-3(-4) $\mu$ , little branched and with few cross-walls; growth at constant temperatures 4.7 cm., 21°; 6.5 cm., 26°; 6.0 cm., 31°; 2.5 cm., 36°; strong reaction with tannic acid medium.

In 14 days mat homogeneous, evenly ochraceous tawny to buckthorn brown, closely compacted, appressed, nodulose, felty to felty-cottony, separating cleanly from underlying agar in thick felted sheets; odor sweetish, resembling wintergreen, most pronounced when cultures are grown in the dark.

*Test tube cultures.* In 4 weeks, mat felty-cottony, evenly buckthorn brown to Dresden brown, no pad formed.

*Distinguishing characters.* *F. igniarius* var. *laevigatus* may be distinguished from *F. igniarius* by its more rapid rate of growth and by its characteristic odor when grown in the dark.

#### 14. FOMES IGNIARIUS var. NIGRICANS Fries.

The various isolates designated *F. igniarius* var. *nigricans* showed no close agreement as to cultural characters. Some were readily recognizable as *F. igniarius* var. *laevigatus* while others differed but slightly from the typical *igniarius*. Until a study can be made of more isolates of the resupinate form of *igniarius* called the *nigricans* variety, it will be impossible to state whether or not a distinct species exists recognizable by cultural characteristics.

#### 15. *Fomes igniarius* var. *populinus* (Neuman) n. comb. Type culture: 16431-S. Figures 44-47, 112.

Growth extremely slow, mat 1-2 cm. in 7 days, variable, compacted, appressed vinaceous brown and haematite red to Brussels brown and raw umber, individual isolates either solidly one color or a combination of several, usually with a fairly distinct, narrow, white to yellowish border; surface of mat covered with a thin to heavy, short-velvety to downy, superficial covering which may be same color as mat proper or somewhat lighter; margin proper narrow, colorless, very closely appressed, even; mat usually producing heavy brown diffusion zone in ordinary malt agar; globose to ellipsoid or irregular-shaped swellings fairly common in some cultures on colored hyphae; hyphae in general show a gradual gradation from submerged thin-walled colorless type to brown superficial type, submerged 3-4(-7) $\mu$ , thin-walled, many cross-walls, much branched, often broken up into short lengths by empty cells, older hyphae yellowish in ap-

pearance, non-staining with ellipsoid swellings, empty hyaline hyphae also common, often showing constrictions at cross-walls; on surface of cultures short lengths of dark, thick-walled hyphae common in some isolations rare in others, 3-4 $\mu$ ; growth at constant temperatures 1.5 cm., 21°; 2.0 cm., 26°; 1.0 cm., 31°; trace 36°; strong reaction with tannic acid medium.

In 14 days mat 1.5-4 cm., variable, closely appressed, compacted, raw sepia to Brussels brown with at times a distinct lighter colored marginal zone, at times appearing much as reduced forms of *F. igniarius* with pronounced two-zoned mat; odor very pronounced, characteristic, sweet, agreeable.

*Test tube cultures.* Poor growth in 4 weeks, mat much appressed, dark, with strong diffusion zone in agar.

*Distinguishing characters.* On growth rate alone *F. igniarius* var. *populinus* can be confused only with *F. robustus* var. *tsugina* and possibly with *F. conchatus*. Odor is sufficient to distinguish it from the ones mentioned while resemblance to the typical *igniarius* will help to distinguish the individual isolations that grow at a faster rate than the usual *Populus* form.

16. FOMES JUNIPERINUS (Schrenk) Sacc. & Sydow Description based on F-3765. Figures 48, 49.

Growth extremely slow, mat 1 cm. in 7 days, homogeneous, appressed, fine woolly-cottony, olive buff to deep olive buff over inoculum, white at margin, usually producing strong diffusion zone in agar; submerged hyphae and colorless superficial hyphae 2-4 $\mu$ , clamps abundant; yellow superficial hyphae 2-3 $\mu$ , non-staining, darkening in KOH, thick-walled and with clamps; constant temperature studies unsatisfactory as fungus makes little measurable growth in 7 days, growth checked above 31°; strong reaction with tannic acid medium.

In 14 days mat 1.5 cm., center olive buff to deep olive buff, marginal portions white or yellowish; odorless.

*Test tube cultures.* In 4 weeks producing a fine woolly to velvety, olive buff to antimony yellow mat, fragile, homogeneous.

*Distinguishing characters.* *Fomes juniperinus* as here described may be separated readily from all other *Fomes* producing clamps by its fine woolly mat, by its olive buff color, and by its slow rate of growth.

17. FOMES LOBATUS (Schw.) Cooke. Type culture: FP-57032-S. Figures 50-53, 113.

Growth slow, mat 2.5-4 cm. in 7 days, definitely two-zoned, central zone appressed, white to yellowish, compacted, often wrinkled, pulveru-

lent to pruinose; marginal zone white, loosely cottony with radiating growth lines in sharp contrast to amorphous central zone; margin proper colorless to faintly white, appressed, fimbriate; submerged hyphae 2-4 ( $-5$ ) $\mu$ , clamps common; superficial hyphae 2-3 $\mu$ , hyaline, non-staining; cuticular cells common in central zone; staghorn branches on surface hyphae, hyaline, readily broken off; growth at constant temperatures 3.5 cm., 21°; 5.0 cm., 26°; 4.0 cm., 31°; 1.0 cm., 36°; strong reaction with tannic acid medium.

In 14 days mat 7-8 cm.; central zone making up most of mat, appressed, much compacted, often wrinkled and furrowed, pulverulent to pruinose or at times covered with scattered patches of short cottony mycelium, solidly avellaneous to buffy brown or only somewhat yellowish in scattered areas that are usually grouped into one or more concentric rings; marginal zone white, cottony; cuticular cells very abundant in central zone; odor variable, faint to prominent, difficult to describe.

*Test tube cultures.* In 4 weeks mat changing from white to yellowish or cinnamon drab on slant, roughened, granular, pulverulent, the portion on agar cylinder irregularly nodulose, cottony, often yellowed with granular masses containing crystals. Deepest colors reached in 8 weeks cinnamon drab to buffy brown.

*Distinguishing characters.* *Fomes lobatus* may be distinguished from all other *Fomes* species producing staghorn branches on superficial mycelium by the dense compacted yellowish to drab central zone containing cuticular cells and by the cottony radiating, white, marginal zone.

18. FOMES MARMORATUS(Berk. & Curt.) Cooke. Type Culture: FP-57058-S. Figures 54-57, 114.

Growth slow, mat 3-4 cm. in 7 days, appressed, thin, faintly to prominently zonate, somewhat cottony with radiating growth lines, uniformly faintly white to somewhat ochraceous or deepening to cinnamon buff and cinnamon, usually with appressed, wrinkled, compacted area about inoculum, cinnamon buff to sayal brown, either localized or extensive, pulverulent, whitish in spots; oidia rare to fairly abundant, in chains of few to several, thin-walled, 3-5 $\mu$  in diameter and in lengths up to 35 $\mu$ ; cuticular cells abundant in compacted areas, thin-walled, colored when mature, up to 25 $\mu$  diameter; submerged hyphae, 2-4( $-6$ ) $\mu$ , clamps abundant; superficial hyphae uniformly 2-3( $-4$ ) $\mu$ , thick-walled, colored or hyaline; growth at constant temperatures 3.8 cm., 21°; 5.7 cm., 26°; 6.5 cm., 31°; 4.6 cm., 36°; moderately strong reaction with tannic acid medium.

In 14 days mat 7-8 cm., appressed, thin, zonate, cottony, faintly white through pinkish buff to cinnamon buff and cinnamon, either evenly

colored or deeper colors confined to irregular patches, center wrinkled, appressed pulverulent, cinnamon buff to sayal brown; no distinct odor.

*Test tube cultures.* In 4 weeks upper part of mat appressed, pulverulent, compacted, Dresden brown to raw umber, separated from white or smoky portion on agar cylinder by a dark, raised line.

*Distinguishing characters.* *F. marmoratus* is the only one of the brown colored species of *Fomes* to produce cuticular bodies in culture. Presence of oidia also very characteristic.

19. *FOMES MELIAE* (Underwood) Murrill. Description based on FP-50236-R. Figures 58-60, 115.

Growth slow, mat 3.5-5 cm. in 7 days, thick, homogeneous, azonate, white, fine velvety-cottony; margin white to colorless, coarsely fimbriate; chlamydospores none or few produced in 7 days, lemon-shaped or ellipsoid  $10-15 \times 6-9 \mu$ ; submerged hyphae  $2-4 \mu$ , clamps abundant; superficial hyphae,  $2-3(-4) \mu$ , hyaline, non-staining; growth at constant temperatures 3.5 cm.,  $21^{\circ}$ ; 4.5 cm.,  $26^{\circ}$ ; 7.0 cm.,  $36^{\circ}$ ; 8.0 cm.,  $36^{\circ}$ ; no reaction with tannic acid medium.

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Explanation of figures 54-98

Figs. 54-57. *F. marmoratus*. 54, Submerged hyphae. 55, Superficial hypha. 56, Oidia. 57, Cuticular cells.

Figs. 58-60. *F. meliae*. 58, Submerged hyphae. 59, Superficial hypha. 60, Chlamydospores.

Figs. 61-63. *F. officinalis*. 61, Superficial hypha. 62, Submerged hyphae. 63, Chlamydospores.

Fig. 64. *F. ohimensis*. Hyphae.

Figs. 65-67. *F. Pini*. 65, Submerged hypha. 66, Superficial hypha. 67, Hyphal swellings.

Figs. 68-71. *F. pinicola*. 68, Submerged hyphae. 69, Superficial hypha. 70, Chlamydospores. 71, Basidiospores.

Figs. 72, 73. *F. rimosus*. 72, Submerged hyphae. 73, Superficial hypha.

Figs. 74, 75. *F. robustus*. 74, Submerged hyphae. 75, Superficial hypha.

Figs. 76-80. *F. roseus*. 76, Submerged hyphae. 77, Superficial hypha. 78, Chlamydospores. 79, Basidia. 80, Basidiospores.

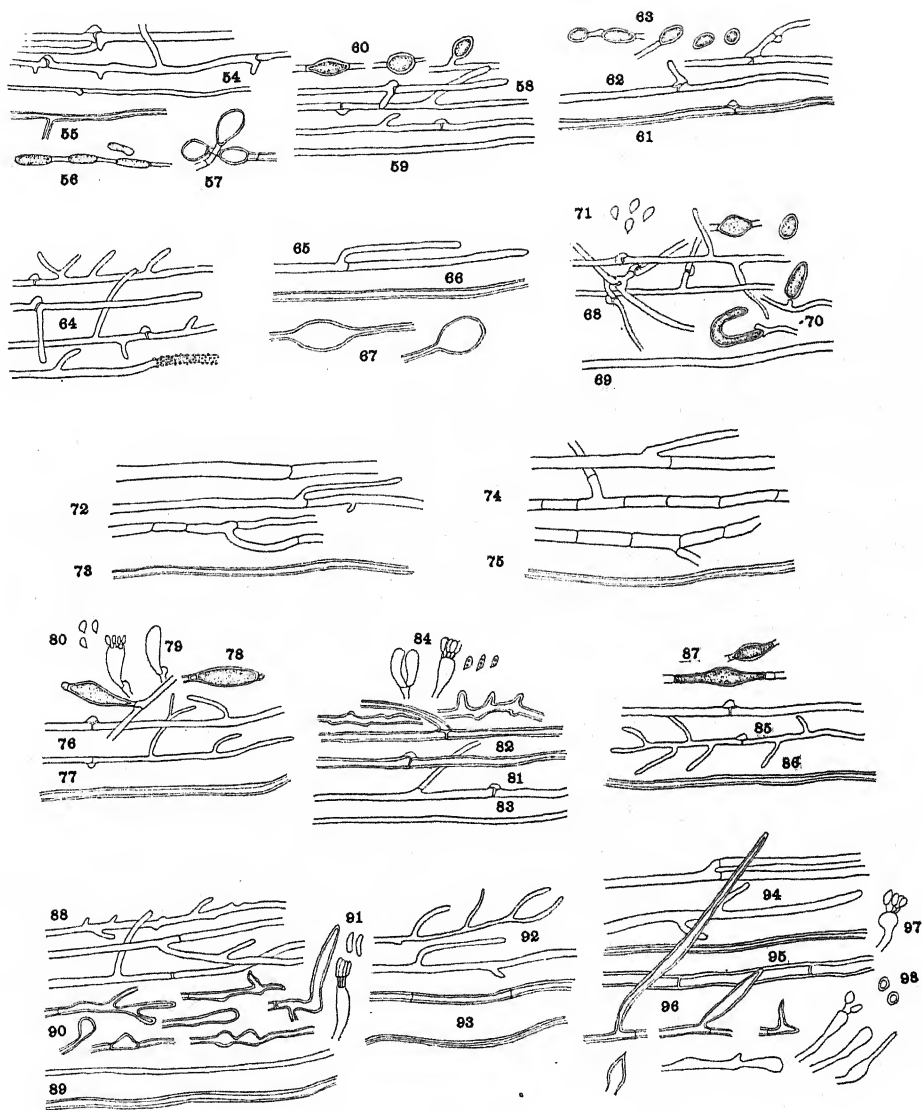
Figs. 81-84. *F. scutellatus*. 81, Submerged hypha. 82, Superficial hyphae. 83, Smaller superficial hypha. 84, Basidia and basidiospores.

Figs. 85-87. *F. subroseus*. 85, Submerged hyphae. 86, Superficial hypha. 87, Chlamydospores.

Figs. 88-91. *F. tenuis*. 88, Submerged hyphae. 89, Superficial hyphae. 90, Irregular hyphal lengths and setae. 91, Basidia and basidiospores.

Figs. 92, 93. *F. torulosus*. 92, Submerged hyphae. 93, Superficial hyphae.

Figs. 94-98. *Sterile Fomes*. 94, Submerged hyphae. 95, Superficial hypha. 96, Setae from surface of mat. 97, Basidia. 98, Basidiospores.



Figs. 54-98. (See opposite page for legend)

In 14 days mat 8 cm. or more, white, finely velvety-cottony, homogeneous, azonate, *forming a heavy gelatinous film on agar*; chlamydospores more common; strong mushroom-like odor.

*Test tube cultures.* In 4 weeks mat white, homogeneous, at times producing fruiting body and mature spores.

*Distinguishing characters.* *F. meliae* differs from all other *Fomes* species here reported except *F. geotropus* in that its optimum temperature is around 36°, and by the tough, gelatinous nature of the film formed on the surface of the agar.

20. *FOMES OFFICINALIS* (Vill. ex Fries) Faull. Type culture: F-1276. Figures 61-63, 116.

Growth very slow, mat 1-2 cm. in 7 days, white, raised woolly to woolly-cottony, homogeneous; azonate, fragile; margin colorless to faintly white, narrow to wide, somewhat appressed fimbriate; chlamydospores numerous, globose to ellipsoid 6-15 $\mu$ , with irregular shaped ones much larger; submerged hyphae 2-5 $\mu$ , clamps abundant; superficial hyphae very similar to submerged hyphae but with slightly thicker walls, 2-5 $\mu$ ; growth at constant temperatures 1.0 cm., 21°; 2.2 cm., 26°; 1.5 cm., 31°; 0 cm., 36°; no reaction with tannic acid medium.

In 14 days mat 2-4 cm., white, raised woolly to woolly-cottony, homogeneous, azonate, fragile; chlamydospores more numerous than at 7 days; odorless.

*Test tube cultures.* In 4 weeks, mat white, nodulose, cottony to floccose on slant, fragile, powdery, rather loosely floccose-cottony on agar cylinder, becoming in time a powdery mass of chlamydospores.

*Distinguishing characters.* *Fomes officinalis* may be distinguished from all other species not reacting with tannic acid by the slow rate of growth and the production of chlamydospores.

21. *FOMES OHIENSIS* (Berk.) Murrill. Description based on FP-52020-S. Figures 64, 117.

Growth very slow, mat 1-2 cm. in 7 days, white or colorless, closely appressed with at times a glazed appearance; margin colorless, even; hyphae essentially of one kind, up to 4 $\mu$ , with abundant clamps; growth too slow to secure satisfactory data 1-2 cm. in 7 days at 21° and 26°, little or no growth at 31° and 36°; strong reaction with tannic acid medium.

In 14 days mat 2-3 cm., dense, very closely appressed, milky white, sometimes cream colored, finely granular to the eye, central portion at times pulverulent, azonate with at times a marked ring paralleling margin; chlamydospores few or none; not abundant until culture has aged con-



siderably; hyphae about center heavily incrustated; odor faint, mushroom-like.

*Test tube cultures.* In 4 weeks mat chalky white to cream colored, appressed, pulverulent, compacted, marginal portion on agar cylinder very finely floccose-cottony.

*Distinguishing characters.* *Fomes ohiensis* may be distinguished from all other reactors with tannic acid medium by its extremely slow rate of growth and by its white color. *F. tenuis* bears some resemblance but becomes definitely colored in 14 days, while *F. conchatus* does not have clamps as does *F. ohiensis*.

22. FOMES PINI (Thore) Lloyd. Type culture: 17553-S. Figures 65-67, 118.

Growth slow, mat 2-3 cm. in 7 days, cultures divided into two forms, one form producing a loose-cottony, raised mat, yellow to ochraceous buff, the other form producing a thick, felted, appressed mat, ochraceous buff, through antimony yellow to yellow ochre; margin proper even, colorless; submerged hyphae  $2.5-4(-5)\mu$ , no clamps; superficial hyphae of two kinds, either white, staining heavily in eosin, with moderately thick hyaline walls, or colored, thick-walled,  $2.5-4\mu$ , often with irregular-shaped swellings which resemble chlamydospores, *in KOH the color diffuses readily turning the solution golden-brown*; growth at constant temperatures 1.7 cm.,  $21^{\circ}$ ; 2.5 cm.,  $26^{\circ}$ ; 2.0 cm.,  $31^{\circ}$ ; trace,  $36^{\circ}$ ; moderately strong reaction with tannic acid medium.

In 14 days mat 3-4 cm., two forms persisting, not much change in appearance; increase in number of hyphal swellings; odor faint, musty.

*Test tube cultures.* In 4 weeks, mat felty-cottony, nodulose, uneven, appressed in spots, cottony pad at times formed on slant, varying from ochraceous buff to yellow ochre and buckthorn brown, pad usually lighter, warm buff to ochraceous buff.

*Distinguishing characters.* *F. Pini* may be distinguished from all other colored species of *Fomes* except *F. conchatus* by the golden yellow color imparted by yellow superficial hyphae to KOH; however, variations in appearance of mat and temperature relations are sufficient to separate *F. Pini* from *F. conchatus*.

23. FOMES PINICOLA (Sw.) Cooke. Type cultures: 16433-S, 15348-S. Figures 68-71, 119.

Growth very variable, mat 3.5-6 cm. in 7 days, either thin and loosely floccose-cottony or rather felty, white, homogeneous; margin thin, colorless or faintly white, coarsely fimbriate; chlamydospores few to numerous, globose to ellipsoid or irregular,  $7-12 \times 5-9\mu$ ; submerged hyphae

2–5 $\mu$ , clamps abundant; superficial hyphae 2–4 $\mu$ , thick-walled, hyaline, without clamps; growth at constant temperatures 4.3 cm., 21°; 6.0 cm., 26°; 7.6 cm., 31°; trace to 1.0 cm., 36°; no reaction with tannic acid medium.

In 14 days mat 7 cm. or more, white, appressed-felty or floccose-cottony to loosely floccose-cottony, forming fairly tough film on agar; submerged hyphae with tendency to break up into irregular shapes not definite enough to be classed as oidia; odor distinct, mushroom-like.

*Test tube cultures.* In 4 weeks, mat white with tendency to verge toward pink or cream color, very fragile, appressed on slant; finely cottony to floccose-cottony on agar cylinder, some isolates forming fruiting structures.

*Distinguishing characters.* *F. pinicola* can be confused with several of the non-reactors on tannic acid media, namely *F. meliae*, *F. subroseus* and *F. roseus*. From *F. meliae* it may be separated on temperature basis since *F. pinicola* barely grows at 36°, while *F. meliae* is near its optimum; from *F. subroseus* by lack of definite vinaceous color of mat and also different shape of chlamydospore; from *F. roseus* by faster growth rate.

24. FOMES RIMOSUS Berk. Type culture: FP-57079-S. Figures 72, 73, 120.

Growth slow, mat 2–4 cm. in 7 days, very thin, fragile, appressed velvety-cottony at center, buckthorn brown or darker to finely floccose-cottony at margin, colorless to mustard yellow, blending with color of agar; margin proper narrow to wide, colorless, very closely appressed, even; submerged hyphae variable in size 3–6(–8) $\mu$ , no clamps; superficial hyphae moderately thick-walled, colored, uniformly 3–4 $\mu$ ; growth at constant temperatures 1.5 cm., 21°; 3.6 cm., 26°; 4.5 cm., 31°; 1.5 cm., 36°; faint to moderately strong reaction with tannic acid medium.

In 14 days mat 4–5 cm., appressed, thin, finely floccose-cottony, buckthorn brown over inoculum becoming lighter toward margin until merging into wide colorless marginal zone; or mat thicker, floccose-cottony, with buckthorn brown or mustard yellow central zone and white, broad marginal zone; odorless.

*Test tube cultures.* In 4 weeks, mat either compacted, felty-cottony or loose cottony, yellow ochre to buckthorn brown, thick, with at times tendency to form shallow poroid areas.

*Distinguishing characters.* *F. rimosus* may be distinguished from other slow growing brown forms by possessing a faster growth rate at 31° than *F. robustus*, *F. Pini*, *F. Calkinsii*, *F. torulosus* and *F. igniarius*. Also the thick, compacted, crumbly mat formed in tube cultures, definitely separates it from *F. robustus*, *F. Calkinsii* and *F. torulosus* which produce

tough thin films on the agar. The mat does not peel from the agar as does *F. igniarius*, and the large size of hyphae separates it from all but *F. robustus*.

25. FOMES ROBUSTUS Karst. Type culture: 16015-S. Figures 74, 75, 121.

Growth slow, mat 2.5–3.0 cm. in 7 days, cultures showing two distinct forms, one form producing a raised, nodulose, finely felty-cottony, to woolly, *azonate* mat, antimony yellow to yellow ochre over center gradually shading to white at margin, the other form compacted, appressed, *zonate*, from buckthorn brown at center to yellow ochre and primuline yellow, with a wide, white, cottony marginal zone; margin proper colorless, narrow, even; submerged hyphae variable in size, 3–6(–7.5) $\mu$ , no clamps; superficial hyphae 2–4 $\mu$ , thick-walled, yellowish brown rough in outline, darkening in KOH; growth at constant temperatures 2.4 cm., 21°; 3.2 cm., 26°; 3.3 cm., 31°; trace 36°; strong reaction with tannic acid medium.

In 14 days mat 5–6.5 cm., raised form evenly warm buff to buckthorn brown, color heaviest over inoculum; appressed form distinctly zoned, warm buff to buckthorn brown, not evenly colored but at times color distributed in relation to concentric zones; odorless.

*Test tube cultures.* In 4 weeks no distinction between forms, all isolates with raised, velvety-cottony to finely woolly fruiting pad on slant, buckthorn brown to yellow ochre; on agar cylinder homogeneous, essentially one color, buckthorn brown, tough, peeling readily from agar.

*Distinguishing characters.* *F. robustus* cannot be separated from *F. Calkinsii* with certainty in either Petri cultures or test tube cultures. In general, *F. robustus* grows at a slightly faster rate, is more vigorous in appearance and is more deeply colored. As far as test tube cultures are concerned, *F. robustus*, *F. Calkinsii*, *F. densus* and *F. torulosus* are practically identical and exhibit no features of value in identification. Temperature relations help to separate it from *F. densus*, but *F. torulosus* is more deeply colored and the submerged hyphae are smaller.

26. FOMES ROBUSTUS var. TSUGINA (Peck) Overh. Type Culture: 16836-S. Figure 122.

Growth very slow, mat 1–2 cm. in 7 days, buckthorn brown to cinnamon brown with a fine, short cottony to woolly, superficial covering, straw yellow to Naples yellow; margin thin, colorless, appressed, fairly broad, even; hyphal characters as for *F. robustus*; strong reaction with tannic acid medium.

Mat in 14 days 3–4 cm., dark brown as seen from underside of dish,

often producing a diffusion zone of considerable extent in agar, with a thin, cottony to woolly superficial covering, ochraceous buff to yellow ochre, mat proper as viewed through superficial covering dark vinaceous brown; *odorless*.

*Distinguishing characters.* On growth rate, color, and reaction to gallic and tannic acids. *F. robustus* var. *tsugina* falls into a group with *F. conchatus*, *F. juniperinus*, *F. igniarius*, var. *populinus* and *F. tenuis*. It may be distinguished from *F. conchatus* on general appearance since it does not produce the white, felty, cottony mat during the first 7 days of growth. *F. juniperinus* is more yellowish and homogeneous than var. *tsugina* and also produces clamps on submerged hyphae. *F. igniarius* var. *populinus* may be separated by its characteristic odor while *F. tenuis* does not form the dark colored mat proper nor the diffusion zone in the agar.

27. FOMES ROSEUS (Alb. & Schw.) Cooke. Type cultures: Snell 10 and 11. Figures 76-80, 123.

Growth slow, mat 3.5-4.5 cm. in 7 days, white to very slightly pinkish or rose-tinted, appressed, floccose-cottony, with mycelium orientated toward center, often definitely plumose, homogeneous, azonate; chlamydo-spores few, irregular in shape and size, with fairly thick hyaline wall, up to  $40\mu$  in length; submerged hyphae  $1.5-3(-4)\mu$ , clamps abundant; superficial hyphae similar with heavier walls and deeply staining contents, or more fibrous, non-staining up to  $4\mu$ ; growth at constant temperatures  $3.5^{\circ}\text{C}$ .,  $21^{\circ}$ ;  $4.0^{\circ}\text{C}$ .,  $26^{\circ}$ ;  $4.5^{\circ}\text{C}$ .,  $31^{\circ}$ ;  $1.5^{\circ}\text{C}$ .,  $36^{\circ}$ ; no reaction with tannic acid.

In 14 days mat 7-8 cm., thin, appressed, floccose-cottony, plumose especially near margin, white over entire surface or rose-tinted over inoculum or over major portion; odor distinct, of green apples.

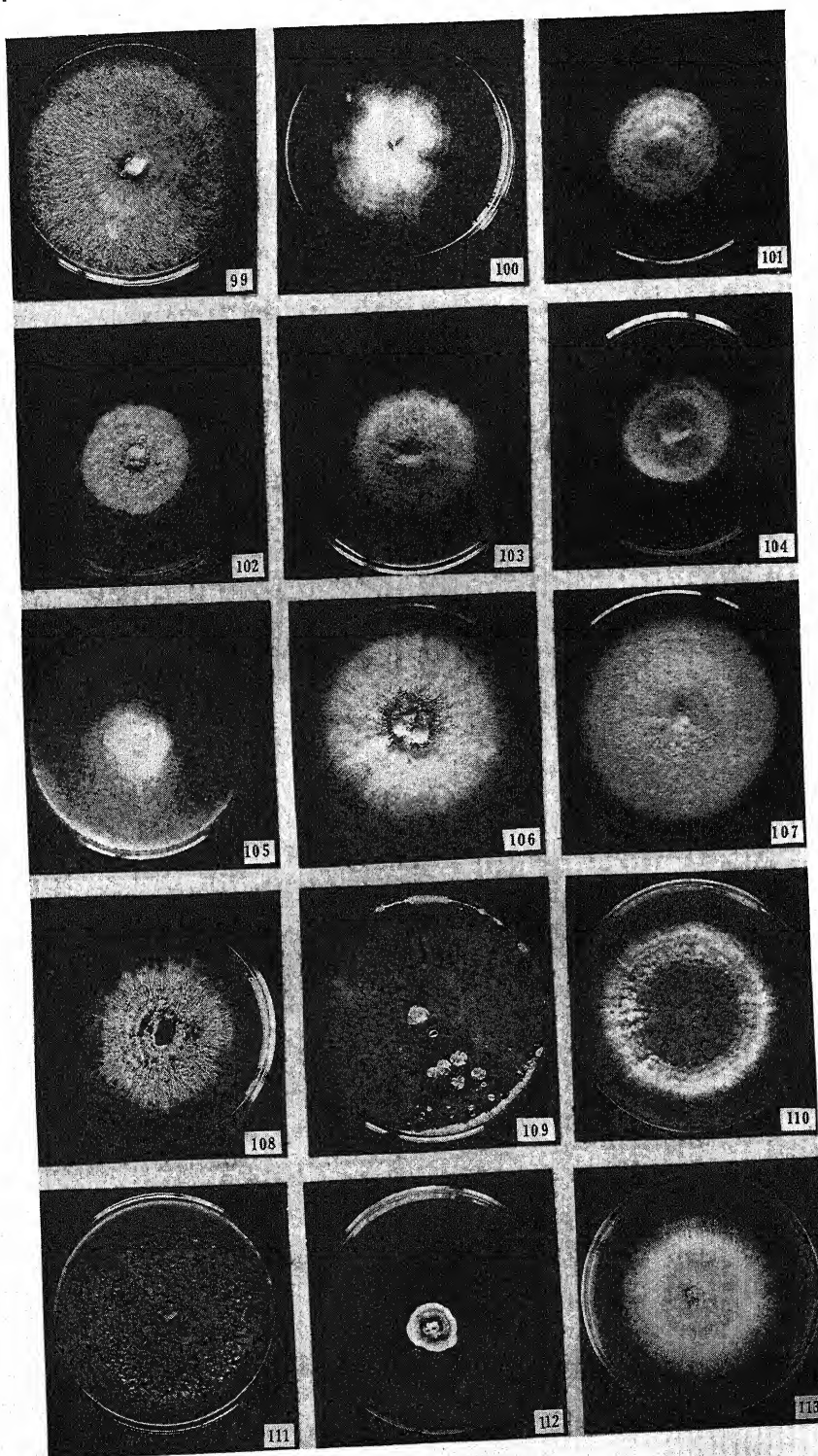
*Test tube cultures.* In 4 weeks mat thin appressed, with definite plumose appearance from pinkish buff through vinaceous cinnamon to as dark as cinnamon over inoculum, rest of mat white, or with indefinite pink or vinaceous tint, fragile.

*Distinguishing characters.* *F. roseus* falls in the same group as *F. pini-cola*, *F. meliae* and *F. subroseus*. However, the slower rate of growth at

#### Explanation of figures 99-113

Mats on malt agar, in diffused light, at room temperature. Age 14 days unless otherwise stated.

Fig. 99. *Fomes annosus*. 100. *F. applanatus*. 101. *F. Calkinsii*. 102. *F. conchatus*. 103. *F. densus*. 104. *F. Everhartii*. 105. *F. fomentarius*. 106. *F. fraxineus*. 107. *F. fraxinophilus*. 108. *F. fulvus*, age 11 days. 109. *F. geotropus*. 110. *F. igniarius*. 111. *F. igniarius* var. *laevigatus*. 112. *F. igniarius* var. *populinus*. 113. *F. lobatus*.



Figs. 99-113. (See opposite page for legend)



31° and the pinkish or vinaceous tints developed in tube cultures definitely separate it from the first two, while Snell's (1928) observation as to growth rate at 31° is the only way to separate it from *F. subroseus*.

28. *FOMES SCUTELLATUS* (Schw.) Cooke. Type culture: 17039-S. Figures 81-84, 124.

Growth slow, mat 2.5-4 cm. in 7 days, isolates showing considerable variation, either with a prominent, appressed, central zone, cinnamon buff to brownish drab and army brown, with white appressed, granular marginal zone; or mat white, loosely felty-cottony, without any or only slight indication of a colored central zone; margin proper also variable, appressed, colorless, fimbriate to more cottony and white; submerged hyphae, 2-4(-5) $\mu$ , with clamps or with thick-walls and deeply staining contents, irregularly branched with short, knobbed sections; superficial hyphae from colored central zone, 2-4 $\mu$ , thick-walled, without clamps; growth at constant temperatures 3.1 cm., 21°; 3.6 cm., 26°; 1.5 cm., 31°; 0 cm., 36°; strong reaction with tannic acid medium.

In 14 days mat 5-9 cm., size dependent upon whether mat remains white and felty without producing a central zone or whether it develops an appressed colored central zone, sayal brown, to army brown and dark greyish brown, both forms producing poroid areas on surface containing well developed basidia and spores; basidia clavate; basidiospores variable, allantoid 6-14 $\times$ 3.5-4 $\mu$ ; paraphyses-like organs found in basidial layer; no odor.

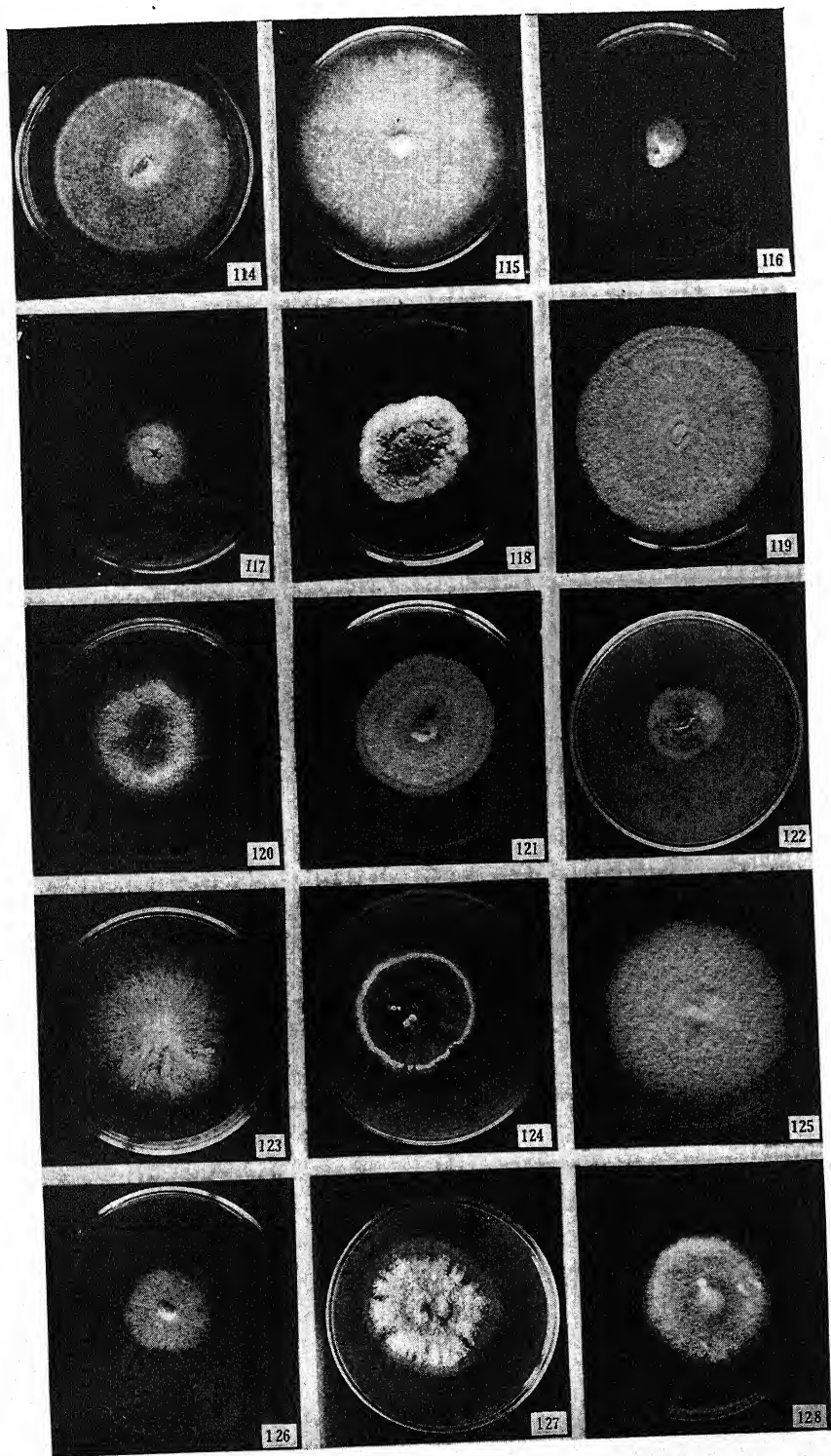
*Test tube cultures.* In 4 weeks mat either remaining white with wood colored or yellowish poroid areas or forming a dark, compacted region on surface of slant, separated from rest by a sharp distinct line, sometimes forming a definite pellicle, with poroid areas developing on colored portion very suggestive of pore surface of *F. scutellatus*; rest of mat white, homogeneous.

*Distinguishing characters.* *F. scutellatus* may appear in several widely differing forms which complicates its identity in culture. If it forms the typical appressed, colored central zone, it may readily be recognized, as no reactor with tannic acid approaches it in appearance; if, however, it remains white and felty, it may superficially resemble *F. fraxineus* and

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#### Explanation of figures 114-128

Fig. 114. *Fomes marmoratus*. 115. *F. meliae*. 116. *F. officinalis*. 117. *F. ohioensis*. 118. *F. Pini*. 119. *F. pinicola*. 120. *F. rimosus*. 121. *F. robustus*. 122. *F. robustus* var. *tsugina*. 123. *F. roseus*, age 11 days. 124. *F. scutellatus*. 125. *F. subroseus*, age 11 days. 126. *F. tenuis*. 127. *F. torulosus*. 128. Sterile *Fomes*.



Figs. 114-128. (See opposite page for legend)

*F. fraxinophilus*, but as it never produces chlamydospores may be readily separated. In test tube cultures, the production of basidia and characteristic allantoid spores coupled with the possible formation of a pellicle, makes it easy to identify.

29. *FOMES SUBROSEUS* (Weir) Overh. Type cultures: Snell-20, FP-57047-S. Figures 85-87, 125.

Growth fairly rapid, mat 4.5-6 cm. in 7 days, chalky white to pink or rose tinted, fairly thick nodulose-cottony to tufted floccose-cottony or felty, homogeneous, azonate, often with poroid areas; margin wide, colorless, appressed, fimbriate; chlamydospores few, lemon-shaped to elongate,  $15-45 \times 6-9\mu$ ; submerged hyphae  $2-4\mu$ , thin-walled, clamps abundant; superficial hyphae with thicker walls, deep staining contents, clamped  $2-4\mu$ ; growth at constant temperatures 4.5 cm.,  $21^\circ$ ; 6.0 cm.,  $26^\circ$ ; 6.5 cm.,  $31^\circ$ ; 2.5 cm.,  $36^\circ$ ; no reaction with tannic acid medium.

In 14 days mat appressed to raised, floccose-cottony to tufted floccose-cottony, homogeneous, azonate, white at margin to irregularly light vinaceous fawn or fawn color, often with distinct poroid areas confined to inoculum or covering most of surface; chlamydospores more numerous; mature basidia rare; basidiospores short cylindric,  $5-8 \times 2-3.5\mu$ ; odor distinct, that of green apples.

*Test tube cultures.* In 4 weeks mat on slant either appressed, floccose-cottony, or raised, with pad on upper part of slant; pores when developed pale ochraceous buff; mat faintly pinkish with upper part light vinaceous fawn. In 8 weeks becoming light ochraceous salmon to light vinaceous fawn.

*Distinguishing characters.* *F. subroseus* may be distinguished from *F. roseus* by its much faster rate of growth at  $31^\circ$ .

30. *FOMES TENUIS* (Karst.) Type culture: 17413-S. Figures 88-91, 126.

Growth slow, mat 1.5-2.0 cm. in 7 days, closely appressed, finely floccose-cottony, indeterminate in color, greyish white to somewhat yellowish; margin proper colorless, slightly fimbriate; hyphal swellings common, resembling chlamydospores; submerged hyphae,  $2-3(-4)\mu$ , no clamps; on older portions of mat much branched and contorted; superficial hyphae up to  $4\mu$ . thick-walled, colored, very irregular, often in short lengths with many branches and swellings; growth at constant temperatures 1.5 cm.,  $21^\circ$ ; 2.0 cm.,  $26^\circ$ ; trace at  $31^\circ$ ; strong reaction with tannic acid.

In 14 days mat 3-4 cm., white to cream or ochraceous buff and cinnamon, appressed, finely woolly to appressed downy, fragile, with at times scattered poroid areas; basidia long, clavate,  $4-5.5\mu$  in diameter, with



sterigmata up to  $4\mu$ ; spores long, cylindric, slightly curved,  $6-8 \times 2-3\mu$ ; superficial hyphae often producing dark brown setae  $4-6\mu$  in diameter, in connection with poroid areas; odorless.

*Test tube cultures.* In 4 weeks mat appressed, compacted, yellowish to ochraceous buff, with heavy poroid areas on slant. In 8 weeks darkest colors sayal brown to cinnamon brown.

*Distinguishing characters.* Of the slow growing *Fomes* species producing a brown zone with tannic acid media, *F. tenuis* may be confused with *F. conchatus*, *F. ohiensis* and *F. robustus* var. *tsugina*. However, *F. ohiensis* produces abundant clamps, while *F. conchatus* is more raised, felty-cottony, and color of superficial hyphae will diffuse in KOH, while *F. robustus* var. *tsugina* is more deeply colored and has larger hyphae.

31. FOMES TORULOSUS (Pers.) Lloyd. Description based on FP-50278-R. Figures 92, 93, 127.

Growth slow, mat 2.5-4 cm. in 7 days, dense, felty-cottony to woolly, faintly to strongly zonate, color homogeneous, very slightly pale yellow at margin to yellow ochre and buckthorn brown at center; margin colorless, fairly broad, even; submerged hyphae  $2-4\mu$ , no clamps; superficial hyphae,  $3-4\mu$ , brown, thick-walled; growth at constant temperatures 2.0 cm.,  $21^\circ$ ; 3.5 cm.,  $26^\circ$ ; 3.5 cm.,  $31^\circ$ ; trace  $36^\circ$ ; strong reaction with tannic acid medium.

In 14 days mat 5-7 cm., center dense, felty-cottony, marginal portions more appressed cottony, zonate, antimony yellow to raw sienna; odorless.

*Test tube cultures.* In 4 weeks mat felty cottony on agar cylinder to loose cottony on slant, often forming loose cottony pad on slant, color homogeneous, between yellow ochre and buckthorn brown, forming a tough film on agar.

*Distinguishing characters.* *F. torulosus* resembles quite closely several of the yellow to brown species of *Fomes* in its cultural characteristics. In general, *F. torulosus* is uniformly darker, buckthorn brown, while *F. robustus*, *F. Calkinsii*, *F. rimosus*, *F. densus* and *F. igniarius* are lighter in color and possess distinct marginal zones.

32. STERILE FOMES Type culture: 17352-S. Figures, 94-98, 128.

Growth slow, mat 2-3 cm. in 7 days, white, raised, loosely cottony, fragile; margin white, cottony, fimbriate; submerged hyphae  $3-6\mu$ , thin-walled, no clamps; superficial hyphae small, thick-walled, non-staining,  $1.5-3\mu$ ; growth at constant temperatures 3.0 cm.,  $21^\circ$ ; 3.0 cm.,  $26^\circ$ ; 2.0 cm.,  $31^\circ$ ; trace  $36^\circ$ ; strong reaction with tannic acid medium.

In 14 days mat 5-6 cm., white to cream buff or yellowish, raised,

loosely cottony, fragile with scattered yellowish patches, usually containing immature basidia associated with setae and slender paraphyses-like organs; surface of culture producing numerous long setae, readily visible under low-power of microscope and turning reddish when touched with KOH; basidia few to rather numerous, clavate or subglobose, up to  $8\mu$  diameter, 2- or 4-spored; spores hyaline, globose to ellipsoid, up to  $8\mu$  diameter; setae  $5-8\mu$  diameter, projecting up to  $25\mu$  in hymenial layer, on surface up to  $130\mu$ ; odorless.

*Test tube cultures.* Mat appressed, yellowish at margin to antimony yellow where best developed, usually producing a large irregular shaped sporophore on slant; poroid areas in cross section show an agglutinated, yellowish mass, without basidia and with numerous short setae lining tubes; no functional basidia seen in abortive sporophores produced in tube cultures.

*Distinguishing characters.* The sterile fungus on *Betula* may be distinguished in culture by its light yellowish color, by the long setae on surface which turn reddish in KOH, and by the abortive sporophore produced in tube cultures.

#### KEY TO SPECIES OF FOMES CULTURED ON MALT AGAR

- |   |                         |
|---|-------------------------|
| Mat white, often varying from faintly white to chalky white, rose colored, or at times somewhat cream colored (14 days).....  | 1                       |
| Mat colored, yellow to brown (14 days).....   | 15                      |
| 1. Clamp connections present.....   | 2                       |
| Clamp connections absent.....   | 12                      |
| 2. Forming brown zone with tannic acid medium.....  | 3                       |
| Not forming brown zone with tannic acid medium.....   | 8                       |
| 3. Growth greater than 3 cm. in 7 days at $26^{\circ}$ C in dark.....   | 4                       |
| Growth less than 3 cm. in 7 days at $26^{\circ}$ C in dark.....   | <i>F. ohioensis</i>     |
| 4. With staghorn branches on the superficial mycelium.....  | 5                       |
| Without staghorn branches on the superficial mycelium.....  | 7                       |
| 5. Chlamydospores present; fruiting readily in test tube cultures, the pore surfaces vinaceous.....                           | <i>F. fraxineus</i>     |
| Chlamydospores not produced; not fruiting readily; cuticular bodies present in mats 14 days old.....                          | 6                       |
| 6. Compacted central zone white or cream colored; marginal zone usually appressed colorless.....                              | <i>F. applanatus</i>    |
| Compacted central zone yellow to avellaneous or buffy brown; marginal zone usually white, cottony, radiating.....             | <i>F. lobatus</i>       |
| 7. Pores almost always produced in tube cultures; chlamydospores numerous, of two kinds.....                                  | <i>F. fraxinophilus</i> |
| Pores never produced in tube cultures; chlamydospores very rare, usually absent.....  | <i>F. fomentarius</i>   |
| 8. Growth 1-3 cm. in seven days at $26^{\circ}$ C.....  | <i>F. officinalis</i>   |
| Growth greater than 3 cm. in seven days at $26^{\circ}$ C.....  | 9                       |
| 9. Forming a gelatinous layer on agar; optimum about $36^{\circ}$ C, forming a mat 8 cm. in diameter at that temperature..... | <i>F. meliae</i>        |
| Not forming a gelatinous layer on agar, growth inhibited or stopped at $36^{\circ}$ C.....                                    | 10                      |

10. Remaining white in cultures 14 days old; test tube cultures also white or slightly yellowish at 4 weeks. . . . . *F. pinicola*  
 Becoming rose tinted or pinkish in 14 days; mats in test tubes becoming as dark as vinaceous-cinnamon or cinnamon. . . . . 11
11. Growth averaging 6.5 cm. in 7 days at 31° C. (dark). . . . . *F. subroseus*  
 Growth averaging 4.5 cm. in 7 days at 31° C. (dark). . . . . *F. roseus*
12. Producing numerous conidia on subglobose conioophores. . . . . *F. annosus*  
 Not producing conidia. . . . . 13
13. Growth at 26° C. more than 6 cm. in 7 days, averaging 15 cm. . . . . *F. geotropus*  
 Growth at 26° C. less than 6 cm. in 7 days. . . . . 14
14. Mat raised, felty-cottony, at times forming rather definite dark colored mat proper; growth about 2 cm. in 7 days. . . . . *F. conchatus*  
 Mat appressed, thin, downy; hyphal swellings common; often producing basidia and spores in tube cultures; growth 2 cm. in 7 days. . . . . *F. tenuis*  
 Mat white, felted, averaging 4 cm. in 7 days; usually forming sporophore in tube cultures. . . . . *F. scutellatus*
15. Clamps present. . . . . 16  
 Clamps absent. . . . . 20
16. Growth slow, less than 2 cm. in 7 days at 26°; mat not producing diffusion zone in agar; color olive buff. . . . . *F. juniperinus*  
 Growth more rapid, more than 3 cm. in 7 days at 26°; mat producing diffusion zone in agar, not yellowish in color. . . . . 17
17. Growth entirely inhibited at 36°; no cuticular cells formed. . . . . 18  
 Growth slight to vigorous at 36° (1 cm. or more in 7 days); cuticular cells formed. . . . . 19
18. Growth 6 cm. in diameter in 7 days at 31°; never fruiting in culture; entire surface of mat colored in tube cultures; thick-walled hyphae uniform, 1-4  $\mu$ . . . . . *F. fomentarius*  
 Growth 1.5 cm. in diameter in 7 days at 31°; usually fruiting in culture; test tube cultures either entirely white or with colored portion confined to upper part; thick-walled hyphae often with short irregular knobs and branches. . . . . *F. scutellatus*
19. Good growth at 36°, 4 cm. or more; oidia present; mat not divided into definite central and marginal zones. . . . . *F. marmoratus*  
 Slight growth at 36°, 1-2 cm.; only central zone colored; no spores of any kind produced. . . . . *F. lobatus*
20. Growth 5 cm. or greater in 7 days at 26°. . . . . 21  
 Growth less than 5 cm. in 7 days at 26°. . . . . 22
21. Mat tough, felted, two-zoned at 7 days, when old peeling readily from agar; odor of winter-green. . . . . *F. igniarius* var. *laevigatus*  
 Mat thin, short-cottony, homogeneous, evenly colored; not peeling readily from agar. . . . . *F. fulvus*
22. Yellow of colored portion of mat diffusing readily in KOH. . . . . 23  
 Yellow of colored portion of mat not diffusing in KOH. . . . . 24
23. On hardwoods only; growth practically stopped at 31°. . . . . *F. conchatus*  
 On coniferous woods; growth averaging 2 cm. at 31°; hyphal swellings common. . . . . *F. Pini*
24. Growth slow, forming a mat 2 cm. or less in 7 days at 26°; color diffusing at times from mat into agar; mat proper dark. . . . . 25  
 Growth more rapid than 2 cm. in 7 days at 26° or if 2 cm. not forming dark mat proper or diffusion zone in agar. . . . . 26
25. Mat proper reddish-brown; superficial growth thin; usually on *Tsuga*; no odor. . . . . *F. robustus* var. *tsugina*  
 Mat proper dark; superficial growth thin to fairly dense, often with a definite border; odor pronounced sweetish; only on *Populus*. . . . . *F. igniarius* var. *populinus*  
 Mat thin, homogeneous, not forming dark mat proper; mat ochraceous buff to cinnamon; no odor. . . . . *F. tenuis*

26. Mat felted, usually two-zoned, center colored, marginal zone white; when 14 days old peeling from agar in a clean sheet leaving whitish film attached. . . . . *F. igniarius*  
 Mat more woolly, not peeling readily from agar, or if peeling from agar, lacking the two-zoned mat and not leaving a whitish film attached. . . . . 27
27. Found only on *Robinia*; mat thin and appressed in light; test tube cultures not forming a fruiting pad nor forming a tough mat on agar. . . . . *F. rimosus*  
 Found only on *Prunus*; mat thin, essentially one color, appressed; fruiting at times readily. . . . . *F. fulvus*  
 Found on a variety of hosts; forming definite fruiting pads on malt agar in test tubes or forming sporophores. . . . . 28
28. In light usually forming a dark mat proper on agar; superficial covering silky, often with a greenish tinge; mat when 14 days old turning vinaceous when rubbed with KOH; on oak. . . . . *F. Everhartii*  
 In light usually not forming a dark mat proper, or if so, superficial covering without greenish tinge; mat woolly to woolly-cottony. . . . . 29
29. Growth at 31° in dark never as great as 4 cm. in 7 days, very slight or no growth at 36° . . . 30  
 Growth at 31° in dark more than 4 cm. in 7 days; fair growth, 1-2 cm., at 36°; mat in 14 days never darker than primuline yellow; superficial covering turning reddish-brown when touched with KOH. . . . . *F. densus*
30. Setae common on surface of culture; basidia and basidiospores often produced in scattered areas, sterile sporophore usually formed in tube cultures. . . . . *Sterile Fomes*  
 Not fruiting in culture; never producing basidia and setae. . . . . 31
31. Hyphae large, up to 7.5μ; mats usually with indefinite white margin. . . . . *F. robustus*<sup>3</sup>  
*F. Calkinsii*  
 Hyphae smaller, rarely larger than 4μ; mats usually darker in color and lacking a definite white margin. . . . . *F. torulosus*

## GENERAL DISCUSSION

*Macroscopic characters.* In the case of fungi in culture, three possibilities suggest themselves in making separations between groups or between individual species within a group, namely: macroscopic features, or those gross differences in color, texture of mat and the like which are readily visible to the naked eye; microscopic characters, or in reality the actual structural characters as revealed by suitable magnification and staining; and lastly the little known differences which may be classified under physiological reactions.

A brief review of the suggested macroscopic characters, as originally stated by Long and Harsch and further studied by Fritz shows that the following have been considered as being of special importance:—rapidity

<sup>3</sup> In general *F. robustus* and *F. Calkinsii* resemble each other too closely to be separated on basis of description alone. Certain differences, however, do exist which enable one acquainted at all with the two species in culture to distinguish them. The *F. robustus* form on *Betula* is particularly distinct but the form on oak resembles *F. Calkinsii* to the extent that one is justified in doubting that any distinction should be made between the two species. *F. robustus*, however, grows at a slightly faster rate, produces a more vigorous mat, and is more strongly colored. In cultures kept in the dark these distinctions are more apparent as *F. Calkinsii* has a tendency to remain pale and delicate while *F. robustus* becomes colored and forms a vigorous woolly mat. Even at the best, however, these differences are in degree rather than on specific points.

of growth; color of aerial and submerged mycelium; character of mat as to texture, form, etc.; staining and discolorations of the agar; and the comparative rates of growth between aerial and submerged hyphae. An attempt will now be made to evaluate these suggested criteria in light of their helpfulness in distinguishing between different species of *Fomes*.

In a general survey of any considerable number of fungi in culture probably the most apparent differences between species would be variations in color. Mycelial mats of *Fomes* species vary from colorless or pure white to all shades of yellow and brown. Usually mats that are inherently colorless or white will remain that way no matter how long they are grown, while those becoming colored will at times start as white mycelial patches later acquiring a characteristic color. Usually this color will develop in a definite period of time. This suggests the division of the species of *Fomes* into a white or colorless section and a colored section, meaning by colored some shade of yellow or brown, allowing a definite time limit, say fourteen days, for the cultures to develop. This procedure separates the species quite satisfactorily, but leaves a minimum number of species which are somewhat indefinite in regard to color and which for this reason must be included in both arms of the key.

After color, rapidity of growth, expressed in colony diameter in a definite period of time, offers most promise for identification purposes. The different species of *Fomes* show growth rates with considerable variations, which when correlated with color give valuable information as to identity. However, since room temperature measurements may show much variation constant temperature measurements are to be preferred.

Texture and type of mat produced offer valuable aids in classification of species. As little can be gained by a multiplicity of terms, Long and Harsch's original list has been followed with few additions. This list has been given under *Description of cultures*. After a little practice one becomes quite proficient in classifying the different cultures under the headings given.

Other suggested characters, such as marginal features, discolorations of the agar, distinctions between aerial and submerged hyphae and the like are too vague to be of much value as far as separation of *Fomes* species is concerned.

*Microscopic characters.* As reported by several workers the list of important microscopic characters includes: septations, branching, size and color of hyphae, presence or absence of clamp connections, polymorphism in spore formation and possibly number and kind of crystals produced in the medium as a result of the metabolic activities of the fungus. In a study of any group of fungi one would hardly expect that the various



microscopic characters would all be of the same importance, and it is quite possible that the value of the different characters varies from group to group. With this in mind an attempt was made to evaluate these characters in relation to the identification of the species of *Fomes* in culture.

Clamp connections with very few exceptions are either present in sufficient numbers as to be readily seen in a microscopic examination or are entirely absent. This makes entirely feasible a division of all species into those with clamps and those without clamps. Appreciable differences in type of clamp produced were not observed although some variation is apparent.

The production of secondary spores in culture adds another possible criterion for the separation of species. These secondary spores may be any one of three types. If, as in *Fomes annosus*, they are produced on definite modifications of the usual hyphal structure, they are designated as *conidia*. If they occur as pyriform or globose inflations of ordinary hyphal cells, produced terminally or intercalary, they are designated as *chlamydospores*. In one species, secondary spores of elongated form (oblong or short cylindric) have been noted. They are regarded as *oidia*. The production of spores varies somewhat with different strains of a given species and with changes in environmental factors. They may, however, be regarded as reliable criteria for purposes of identification, especially when correlated with other factors.

Other microscopic criteria of value for supplementary or correlative information include: presence or absence of staghorn branching; hyphal swellings of various kinds; setae on surface of cultures or in connection with hymenial layers, incrustations of the hyphae; presence or absence of cuticular or vesicular cells; and production of typical basidia and basidiospores.

Hyphal sizes are of little value. In general very little variation occurs between the different species, and what differences do occur are not distinct enough to be reliable. Type of branching is also an uncertain criterion as, although differences in branching do occur, these differences are difficult to describe and apt to be disturbed in the preparation of the specimens for examination. Differences in type of crystals produced are also elusive details which offer but little promise in the separation of the *Fomes* species here reported.

*Response to light.* The effect of the intensity of light on the form and coloration of the mats in cultures were also studied to considerable extent. In general, light has a suppressing effect on the mycelium, which is probably to be expected, and also influences the development of color. A certain amount of light is necessary for the best development of color and

cultures grown for purposes of identification are best treated when exposed to moderately strong diffused light. Growth rate varies considerably as not all species react the same to light. In the dark, the mass of mycelium produced is apt to remain relatively undifferentiated and for this reason furnish few characters of value in identification.

*Temperature relations.* All cultures studied were subjected to constant temperature treatment at temperatures of 21°, 26°, 31° and 36° C. These temperatures were chosen as a matter of convenience and are ones which could be most easily maintained at the time the work was carried on. The treatment of cultures during the course of constant temperature experimentation has been given under *Materials and methods*.

Each individual isolate reacts in a characteristic way as far as growth rate is concerned at a given temperature. While each isolate of a given species maintains its own constant rate of growth, the range expected for any species may be expressed within certain limits. The growth rates given for a species at a particular temperature will be the average of the different isolates.

No attempt was made to separate species into low, medium, or high temperature groups, although this can readily be done from descriptions of individual species. Most cultures of *Fomes* show a preference for temperatures between 25 and 30° C., with few able to grow vigorously at 36° C.

At higher temperatures, individual differences in strains or isolates become most apparent. Also slight variations in moisture and experimental handling produce the greatest chances for possible error.

Since intensity of light made considerable difference in colony diameter in a given time, cultures grown under constant temperature conditions, in dark, cannot be compared with cultures kept in light under same temperature conditions.

*Reactions with special media.* Bavendamm's procedure for detection of white rot fungi and brown rot fungi described under *Materials and methods* offers a simple means for the classification under these two heads. The brown diffusion zone produced as result of reaction with tannic and gallic acid seems constant for each species. Tannic acid is to be preferred as it turns malt agar white, against which the colored diffusion zone shows up to best advantage.

#### SUMMARY

1. Thirty-one species of *Fomes* were studied in detail as to their cultural characteristics.
2. The different species of *Fomes* in culture produce distinct characteristics, which makes their identification fairly certain.

3. The reaction of each species to the culture medium, if conditions remain constant, is distinct and invariable within certain limits. Variations do exist within a given species, these variations being greater in some species than in others.

4. Individual isolates of a given species retain their peculiarities for indefinite periods in culture. There appears to be no sharp change in reaction at any time and individual strains can be depended upon to remain constant.

5. There is no difference between cultures of the same individual prepared from rot or from the sporophore.

6. Macroscopic features of value in the identification of *Fomes* species in order of importance are: color of mat; rate of growth as given in terms of diameter of colony at some definite time interval; texture of mat and production of colored zones; and odor may at times be distinctive.

7. Microscopic features of value in the identification of *Fomes* species in order of importance are: presence or absence of clamp connections; production of secondary spores; existence of supplementary structures such as cuticular bodies, staghorn branches, hyphal swellings, etc.; and hyphal sizes.

8. Most *Fomes* species in culture show a decided response to light evidenced by change in texture of mat, color, and difference in rate of growth. The amount of change depends upon intensity of illumination.

9. The species of *Fomes* differ as to minimum, optimum and maximum temperatures required for growth.

10. Malt agar and potato-dextrose agar are the most suitable media for the culturing of the different species of *Fomes*.

11. Little supplementary data of use in identification can be secured by culturing the *Fomes* species on a wide variety of agars.

12. Tannic and gallic acids when added in 0.5 per cent concentration to regular malt agar furnishes a fairly positive means of distinguishing between white-rot and brown-rot fungi.

13. Cultural studies of fungi are valuable not only in the diagnosis of the cause of decay but also in ordinary taxonomic work in distinguishing between species closely related in external form. Also in distinguishing abnormal or aborted forms of the fungus.

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# INDEX TO AMERICAN BOTANICAL LITERATURE 1935-1937

The aim of this Index is to include all current botanical literature written by Americans, published in America, or based upon American material; the word America being used in the broadest sense.

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## The genus *Cooperia*

H. HAROLD HUME

Bulbs collected by the Scotch plant explorer, Thomas Drummond, in eastern Texas were sent to the Botanic Garden, Glasgow, in 1834, and from there distributed to a number of plant lovers in Scotland and England early in 1835. Among the first flowers produced from these bulbs in Great Britain was one secured by Joseph Cooper, gardener at Wentworth House in Yorkshire, England, the country seat of Earl Fitzwilliam. This estate evidently had plant collections of considerable size as it has been referred to as a botanic garden. With the Wentworth specimen in hand, William Herbert (1836) established the genus *Cooperia* commemorating the name of Mr. Cooper. To the type species the name *C. Drummondii* was given in honor of Thomas Drummond. The illustration (Botanical Register *pl.* 1835) accompanying the description bears the date February 1, 1836.

Among Drummond's bulbs was another belonging to the same group which flowered in the collection of Doctor Neill, Canonmills, near Edinburgh, Scotland, July, 1835. This presented certain characters different from *C. Drummondii*, and D. Don (1836) described it as *Zephyranthes Drummondii* without having seen the living plant. The plate (Sweet, Brit. Fl. Gard. *pl.* 328. 1836) from a drawing by James MacNab, accompanying the description, is dated March 1, 1836. A short time after Herbert had established the genus *Cooperia*, R. Graham (1836) published a description of Don's *Z. Drummondii*, under the name *Sceptranthes Drummondii*, from a flower produced by J. Dickson and Son early in March, 1836. He believed it to be distinct from both *Zephyranthes* and *Cooperia* and pointed out certain respects in which he thought it differed. Later Herbert properly described this plant under *Cooperia* giving it the name *Cooperia pedunculata*, the specific name, *Drummondii*, given by Don and by Graham, having been applied already, as just stated, to another species in the genus.

It is worth noting that three generic names were used, all within a very short period of time: *Cooperia* (February 1, 1836), *Zephyranthes* (March 1, 1836), and *Sceptranthes* (March 10, 1836), evidence of the keen botanical interest in these plants at the time of their first flowering in Great Britain. Priority in establishing the genus belongs to William Herbert.

While *Cooperia* is related to *Zephyranthes* so closely that the two frequently have been confused and hybrids between them have been secured, it is to be separated from the latter genus by the longer perianth-tube, [THE BULLETIN FOR JANUARY (65: 1-78) WAS ISSUED JANUARY 6, 1938]

very short filaments, erect, not versatile anthers, scented flowers, and night-blooming habit.

COOPERIA Herb. Bot. Reg. pl. 1835. F 1836.

*Sceptranthes* Graham, Edinb. New Phil. Jour. 20: 413, 414. Mr. 1836.

Acaulescent herbs with coated bulbs and linear, glabrous, erect, recumbent, or decumbent leaves; flowers borne singly on an erect hollow scape; spathe membranous, tubular in the lower part; perianth white tinged outside with red or green of six parts (three sepals and three petals) partly united below to form a tube, the tube elongate, cylindric or slightly dilated upward; calyx- and corolla-lobes usually spreading; stamens six, with very short triangular filaments, adnate up to the throat of the perianth tube; anthers slender, erect (not versatile); stigmas round-lobed; style filiform; ovary three-celled, sessile or stipitate; capsule membranous, loculicidal, three-lobed; seeds numerous, flattened, thin, black. Flowers produced in spring, primrose scented, opening in the evening.

Though John Lindley published at one and the same time descriptions by Herbert (1836) of two plants in connection with Herbert's definition of the genus, *Cooperia Drummondii* should be regarded as the type. It is given first place in the discussion with a brief note on *C. chlorosolen* added. Later Herbert (1837) placed the latter as a variety of *C. Drummondii*.

In North America, cooperias of one kind or another are native from northeastern Mexico to New Mexico, Kansas and southwestern Louisiana. Outside this area only one other species, *C. albicans*, from Peru, is known.

#### KEY TO COOPERIA

Ovary not stipitate.

Perianth-tube greatly elongate [6.5–18 cm.]: style as long as or longer than the perianth tube.

Calyx- and corolla-lobes relatively broad, imbricate below the middle.

Perianth-limb rather small, less than 4 cm. wide; tube slender, red-tinged; calyx-lobes white. 1. *C. Drummondii*

Perianth-limb large, over 4 cm. wide; tube stout, green; calyx-lobes lined with green within. 1a. *C. Drummondii chlorosolen*

Calyx- and corolla-lobes narrow, not imbricate. 2. *C. Traubii*

Perianth-tube shorter [7–11.2 cm. see descr.]; style much shorter than the perianth-tube: calyx- and corolla-lobes broadly lanceolate, 4–4.5 cm. long. (Peruvian) 3. *C. albicans*

Ovary stipitate

Perianth-tube relatively short [0.5–9 cm.] calyx- and corolla-lobes imbricate; ovary and stipe included in the spathe. 4. *C. pedunculata*

#### 1. COOPERIA DRUMMONDII Herb.

Bot. Reg. 22: pl. 1835. F 1836.

*Cooperia Drummondiana* Herb. Amaryll. 178. 1837.

Bulb large, subglobose, 2×3 cm., the neck 2 to 9 cm. long, not pronounced in some specimens, the tunics black; leaves 2 to 5, narrow, linear, gray-green,

upright or declinate, 2 mm. wide, 30 cm. long; scapes 2 to 3 mm. wide, 10 to 21 cm. long, commonly solitary or two together, gray-green above, shading to reddish-brown below; spathe slender, thin, membranous, pink-tinted, commonly looped at the tip, sometimes bifid, 3.5 to 6 cm. long, 2.3 to 4.2 cm. to the slit; the spathe-tube embracing and extending above the ovary, about one third as long as the perianth-tube; stipe none; perianth-tube slender, elongate, greenish white or pinkish white, 6.5 to 18 cm. long, 2.5 mm. thick; perianth-limb opening flat, or stellate with margins of lobes incurved, white, pink tinted on outer surface, calyx lobes ovate to lanceolate 2.4 cm. long, 1.3 cm. wide, with blunt tips, corolla-lobes 2.2 cm. long, 1.2 cm. wide; stamens erect, filaments white 3 mm. long, 1.5 mm. wide, rectangular in outline, apices concave; anthers erect creamy yellow, 9 mm. long, attached to filaments one third of length from base; ovary almost cylindric, 6 mm. long; style white slightly clavate, 9.5 cm. long reaching to middle of anthers or extending above them; stigmas lobed, the lobes depressed 1 mm.  $\times$  1.5 to 2 mm.; capsule of three rounded depressed lobes, 1 cm.  $\times$  1.5 to 2 cm.; seeds numerous thin, flattened, black, half circular or rounded triangular in outline, 5 mm.  $\times$  8 mm.—Season May–August.

Although there are specimens of *C. Drummondii* collected by Drummond (411) in various herbaria (Kew, British Museum, Edinburgh), a type specimen is unknown. Herbert based his diagnosis upon a fresh flower produced by a bulb collected by Drummond. All of Drummond's herbarium specimens seen are without bulbs. Apparently he removed them before sending his material from Texas. Lindheimer collected the species at an early date, 1847–1849. Herbert had also received bulbs of Drummond's collection which he planted and flowered in his greenhouse at Spofforth, England.

Of all the cooperias known at this time, *C. Drummondii* is the most widely distributed. It is a native plant in northern Mexico and ranges as far north as New Mexico, Kansas, and Louisiana, with its most abundant distribution in Texas.

1a. *COOPERIA DRUMMONDII* var. *CHLOROSOLEN* Herb.

Baker Handb. Amaryll. 27. 1888.

*Cooperia chlorosolen* Herb. Bot. Reg. under *pl.* 1835. F 1836.

*Cooperia Drummondiana* var. *chlorosolen* Herb. Amaryll. 178. *pl.* 24, *f.* 1. 1837.

"Perianth tube stouter, tinged with green; limb longer, less rotate. Leaves a little broader." J. G. Baker (1888).

Herbert secured flowers of *C. Drummondii* in his greenhouse at Spofforth, England, from bulbs collected by Drummond in Texas between the Brazos River and San Felipe (Drummond 411). Another bulb of the same

lot bore leaves and early in January, 1836, produced a flower that differed in some particulars from those of *C. Drummondii*. This plant he described briefly as *C. chlorosolen* (1836) and two months later followed with a colored plate and a longer, more detailed description. At this time he said it "differs from *Cooperia Drummondii* . . . in having a much larger limb, the tube green, and the sepals lined with green on the outside, the leaves longer and wider, the filaments free from the tube one-eighth instead of one-sixteenth and the style shorter than the tube."

Later Herbert (1837) placed his *Cooperia chlorosolen* as a variety of *C. Drummondii* and changed the spelling of the latter specific name without offering any explanation as to why he reduced it to a variety. Baker accepted Herbert's disposition of the plant and supplied the brief description quoted above.

*Cooperia Drummondii chlorosolen* rests solely upon Herbert's original description. Specimens labeled "*chlorosolen*" are in herbaria but they present in their dried state no characters by which they can be distinguished from the species. Features emphasized by Herbert and by Baker, and in a note by Weathers (1911) at a more recent date, "The variety has stouter flower-stems, flowers tinged with green and having less spreading segments" are not sufficient to establish the varietal position of the plant. All descriptions and comments, it appears probable, are based upon the original description by Herbert and no greater variations than are to be found among related plants are indicated. There is need for further field work and a careful study of growing flowering plants and their offspring if they can be secured before it can be determined whether it is actually entitled to varietal rank or whether it may be a species or whether it is only a color variant. Nowhere does Herbert indicate that he had secured more than a single flower of it. The illustrations (*Sceptranthes Drummondii* and *Cooperia chlorosolen*) given by Loudon (1841) show two flowers that are quite distinct in general appearance and *S. Drummondii* is quite different from Herbert's (1836) illustration of *C. Drummondii*.

## 2. COOPERIA TRAUBII Hayward

Am. Amaryll. Soc. 3: 63-66. 1936.

Bulb globose 1.6 cm. diameter; the neck 2.7 cm. long; leaves about four, linear, glaucous, recumbent, to 22.5 cm. long; scape slender, cylindric, 17.5 to 19 cm. long; spathe cylindric, light tan-colored, about one-third as long as the perianth-tube, 4.8 cm. long over all, the tips 1.4 cm. long, slender, acute; stipe none; perianth-tube very slender, cylindric, expanded slightly at apex; perianth-limb star-like, white, faintly tinted pink outside, 5.5 cm. expanded, 15 cm. long including ovary, calyx- and corolla-lobes separated, slightly re-

curved at anthesis, white within, faintly pink tinted on outer surfaces of three sepals lanceolate, rounded at the tips, 3.4 cm. long, 6.9 mm. wide; stamens with very short white filaments; anthers erect, slender, light-colored; ovary 7 mm.  $\times$  5 mm.; style slender, white, 12.5 cm. long; stigmas white, with short rounded lobes expanded 3 mm. elevated about 10 mm. above anthers.—Season June.

This cooperia is known only from the vicinity of Angleton, Texas, where it grows in grassy plains. Bulbs were collected by R. H. Stansel and sent to Dr. H. P. Traub, Orlando, Florida. Flowers were produced in the trial garden of the American Amaryllis Society, Winter Park, Florida. One of these is preserved as the type specimen (1,634,673) in the U. S. National Herbarium. The species is most closely related to *Cooperia Drummondii* Herb., which it resembles in its non-stipitate ovary and length of the perianth-tube, but from which it apparently differs in narrow, slender leaves, larger flowers and separated, somewhat recurved calyx- and corolla-lobes.

### 3. COOPERIA ALBICANS (Herb.) Sprague

Kew Bull. 386. 1928.

*Lilio-Narcissus monanthus flore albicante tubo praelongo* Feuillée, Jour. Obs. (Hist.) 29. pl. 20. (sinistra) 1725.

*Pyrolirion albicans* Herb. Amaryll. 184. 1837.

*Zephyranthes albicans* Baker Amaryll. 38. 1888.

Bulb medium size, subglobose, short-necked in specimens examined, black or dark-brown to brown, 2.5 cm.  $\times$  2 cm., without offsets; leaves 3 on specimen, slender below, widening upward thence tapering to apex, linear-oblancoate, with incurved margins, striations present, 7-nerved, 2.5 to 4.0 mm. wide, 12 to 20 cm. long; scape 1 in specimen, subcylindric, 3.5 to 4.5 mm. wide, 7 cm. long; spathe membranous, 4.2 cm. long, 2.2 cm. to slit, shorter than the perianth-tube, unilateral with slender, acuminate tips; stipe none; perianth-tube slender, 7 cm. long, slightly expanded at summit, 11.2 cm. long, including ovary, greenish-white; perianth-limb white, about 7.5 cm. expansion; calyx-lobes broadly lanceolate, 4 to 4.5 cm. long, 1.7 cm. wide, separated near apex, imbricate near base, white, rounded; corolla-lobes 1.5 cm. wide, some slightly narrower; stamens with flattened deltoid filaments, slightly united toward base, upper parts oblong, tapered to apex, 1 m.  $\times$  0.7 m.; anthers 3 mm. long; ovary oblong, 1 cm.  $\times$  5 mm., style short, about 3 mm.; stigmas spatulate, slightly above the anthers, 3–4 mm. expansion.

*Cooperia albicans*, known in botanical literature under one name or another over a period of more than two centuries, has an interesting history. It was discovered in dry soil at Ylo, Peru. Feuillée (1725) described it under the phrase "*Lilio-Narcissus, flore albicante tubo praelongo.*"



Herbert based his disposition of the plant upon Feuillée's discussion and referred it to *Pyrolirion* as a doubtful species with the name *P. albicans*, at the same time indicating his thought that it might be a *Cooperia*. Roemer (1847) followed Herbert, supplied a brief description and, with a question mark, expressed doubt concerning its classification. Kunth (1850) placed it under *Pyrolirion* as a doubtful species with a brief description based upon Herbert's diagnosis. Baker (1888) transferred it to his *Pyrolirion* section of *Zephyranthes* as *Z. albicans*. There it remained until Sprague (1928) secured fresh flowers from bulbs collected at Mollendo, Peru, furnished by Major Albert Pam. His conclusion that the fresh material belonged with Feuillée's plant and both to the genus *Cooperia* admits of no doubt. Hence the combination *Cooperia albicans* (Herb.) Sprague.

Specimens of this plant in herbaria are not numerous. In addition to those in the herbarium of the Royal Botanic Garden, Kew, there is a fine set in the Museum Botanicum Berolinense. This consists of nineteen more or less complete specimens on four sheets, collected in 1902, by Dr. A. Weberbauer (Flora von Peru 1510), at Mollendo, Peru. There is in the Herbarium Field Museum a specimen, 609,717, of this collection by Weberbauer. It will be noted that in the same locality the bulbs presented by Major Albert Pam to the Royal Botanic Gardens, Kew, from which Sprague secured his flower specimens were collected. The presence of this species far south of the North American area for the genus and on the other side of the equator is of interest to the student of plant geography. Its distribution is paralleled in the related genera *Zephyranthes* and *Habranthus*, species belonging to which are similarly separated.

*Cooperia albicans* is apparently the largest flowered species of the cooperias known at this time. It is quite distinct from others in its wide, reflexed calyx- and corolla-lobes. In its native home it is known as "amancaes" or "flor de amancaes."

#### 4. COOPERIA PEDUNCULATA Herb.

Amaryll. 179. *pl.* 42, *f.* 3. 1837.

*Zephyranthes Drummondii* D. Don Sweet Brit. Fl. Gard. *pl.* 328. Mr 1 1836.

*Sceptranthes Drummondii* Graham Edinb. New Phil. Jour. 20: 413. Mr 10 1836.

Bulb large, torpedo-shaped when young, flattened-globose when old, dark-brown to black, 2.5 cm. × 4 cm.; the neck long, 5-8 cm., both bulb and neck with abundant covering of old sloughing tunics; leaves 4 to 6, linear, 5 to 6 mm. wide, glaucous-green, twisted and recumbent; scapes solitary or 2 or more

together, cylindric, 3 mm. wide, 13 to 16 cm. long, glaucous-green; spathe thin and membranous, sack-like, pink, 3.5 to 4.5 cm. long, 2.2 to 3.7 cm. to slit, the tubular portion extending well above the ovary and completely enclosing it, the tips bifid or looped, attenuated; stipe short, 0.5 to 3.3 cm. long; perianth-tube cylindric, slender, expanded very slightly and gradually upward, 3 to 4 cm. long, with ovary 6.5 to 9 cm. long; perianth-limb broadly funnel-form,<sup>?</sup> expansion 5 cm., white, flushed pink without; calyx-lobes oblong-obovate, 2.7 cm.  $\times$  1.6 cm., imbricate, white flushed pink outwardly, apex rounded-cuspidate; corolla-lobes white tinted pink, rounded at the apex; stamens in two sets of placements, one slightly above the other; filaments short, white, triangular, 1 to 2.5 mm. long, anthers cream-yellow, erect, 6-8 mm. long; stigmas white, rounded, 2 mm. expansion; ovary ovoid, 1 cm.  $\times$  5 mm.; capsule bluntly triangular, 1.6 cm. along each side, 1.5 cm. high, slightly tapering downward; seeds numerous, thin, black, 4  $\times$  7 mm. to 6  $\times$  9 mm.

Compared with *Cooperia Drummondii* the distribution of *C. pedunculata* is restricted. It is found in Texas and in the adjacent parts of Mexico—Coahuila, Nuevo Leon, and Tamaulipas.

Its bulbs are torpedo-shaped when young and amply provided with contractile roots<sup>1</sup> by means of which they are pulled down into the soil. Under garden conditions in Florida's sandy soil, bulbs have been found at a depth of 30 cm., but, judging from the necks of herbarium specimens, they are commonly found at a depth of 8 to 10 cm. under natural conditions. Mature native bulbs are turbinoid, long-necked, and provided with copious sloughing coats. Such coats commonly are associated also with certain species of bulbs, inhabiting dry soils, belonging to the related genus *Zephyranthes*.

#### SPECIES EXCLUDED

#### COOPERIA MEXICANA Herb.

Amaryll. 182. 1837.

*Cooperia mexicana* Herb. was listed by Herbert as a doubtful species, the bulbs and leaves only of which were known to him. It was imported from Mexico by Mr. Loddiges, Hackney, England. Lacking a description of the flower, it is not possible to assign the name to any known plant. *Cooperia mexicana* Herb. must therefore be regarded as a *nomen nudum*. The name has been placed as a synonym (1893) for *C. Drummondii*, but upon what grounds is not apparent.

<sup>1</sup> Contractile roots probably are to be found on bulbs of all species of *Cooperia*. Those of *C. Drummondii* have been the subject of special study by Church (1919).

## COOPERIA MIRADORENSIS Kränz.

Repert. Sp. Nov. 21: 75. 1925.

*Cooperia miradorensis* Kränzlin was based upon a specimen (Liebmann 7925:), consisting of a scape and flower, now in the herbarium of the University of Copenhagen. It was collected by Frederik M. Liebmann in a field at Mirador, Mexico, where he made his headquarters from time to time while collecting plants and herbarium specimens in Mexico for the Botanical Garden of Copenhagen during the period February 7, 1841, to May 6, 1843. Owing to the scanty nature of the material and the difficulty of making out certain features, Kränzlin's description is lacking in important details. Opportunity has not been afforded for examining the original specimen, but through the kindness of Dr. S. C. Simms, late Director, Field Museum of Natural History, a photograph of it has been available. There is nothing in the original description or apparent in the photograph to indicate in what respects this plant is to be set apart from the genus *Zephyranthes*. To this genus it quite apparently belongs and it is so referred here without attempting to indicate definitely the identity of the species. It closely resembles *Z. macrosiphon* Baker, a Mexican species the exact native habitat of which is unknown.

## GARDEN VALUES

Fine flowering clumps of *Cooperia* may be secured in the garden by planting a number of bulbs close together (two to three inches apart) and three to four inches deep. Mature, well grown bulbs usually produce several flowers in spring (April to June). Since they open in the evening and remain open during the night they are valuable in the garden for that time of day and the primrose scent of the flowers is an added attraction. They are easily grown in well drained soils in southern gardens. Bulbs are readily grown from seed and from bulb cuttings. Cooperias of one sort or another are to be found here and there in gardens of the Gulf Coast country. In Florida they have been noted at different points from Key West to Gainesville.

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## Additional Miocene plants from Grand Coulee, Washington

EDWARD W. BERRY  
(WITH EIGHT FIGURES)

In 1931 I published an account of a Miocene flora collected at Grand Coulee, Washington, by several interested citizens of that state.<sup>1</sup>

Since that time I have received material from this same locality from George F. Beck of the State Normal School at Ellensburg, Washington. Mr. Beck is himself making a study of the fossil woods of the state and his results promise to be of the greatest importance not only in themselves but as a check on the identification of the fossil leaves from the associated beds.

Since it seems hardly likely that I will have the opportunity to make any extensive contribution to this fascinating problem, it seems highly desirable to place on record the additional species that have been recognized from Grand Coulee.

The flora thus far discovered at this locality is strikingly similar to that described from the Latah formation of eastern Washington and Idaho and any conclusions regarding its ecology or botanical character would necessarily be similar to those reached from a study of the latter.<sup>2</sup>

The present additions to this flora comprise the following:

*Castanea orientalis* Chaney  
*Castanopsis consimilis* (Newberry) Brooks  
*Cornus Becki* Berry  
*Diospyros Andersonae* Knowlton  
*Fagus pacifica* Chaney  
*Ginkgo adiantoides* (Unger) Heer  
*Juglans oregoniana* Lesquereux  
*Liquidambar californicum* Lesquereux  
*Magnolia Inglefieldi* Heer (?)  
*Magnolia spectabilis* Knowlton  
*Quercus spokaneensis* Knowlton  
*Quercus ursina* Knowlton  
*Rhus Merrilli* Chaney

The following deserve special comment:

*Ginkgo adiantoides* (Unger) Heer

(Figure 2)

*Ginkgo adiantoides* (Unger) Heer, *Flora fossilis arctica*, 5<sup>3</sup>: 21. *pl. 2. f. 7-10*. 1870.

<sup>1</sup> Berry, E. W. U. S. Geol. Survey Prof. Paper 170, pp. 31-42, pls. 11-13, 1931.

<sup>2</sup> Berry, E. W. *Idem*. 154, pp. 225-265, pls. 49-64, 1929.

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Berry, Geol. Survey Canada Bull. 42: 96, Natl. Museum Canada Bull. 63: 18. 1930.  
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Although individually much less abundant than most of its associates the Ginkgo has an unparalleled geographic and geologic range. The leaves are very conservative in their organization and also in their great variability from the Jurassic to the present. Consequently authors differ in their specific segregations. It is customary to refer the leaves found in the Tertiary to *Ginkgo adiantoides* although they are indistinguishable from such Cretaceous forms as *Ginkgo laramiensis* Ward or *Ginkgo pseudoadiantoides* Hollick, or from selected specimens of the existing species.

It seems hardly possible that a single botanic species should continue unchanged through such a vast lapse of time, but if there are specific differences one would hardly expect the specific bounds to coincide with the artificial boundaries of the geologic time scale.

Although I have followed the traditional procedure in the present case, it would seem from the distinctly Asiatic relationship of so many of the associated species that these late Miocene examples from Washington, Oregon and Idaho are more likely to be identical with the living species than with the early Tertiary form which is so widely distributed throughout the Holarctic region. In fact Depape<sup>3</sup> has not hesitated to refer lower Pliocene specimens from France to the existing *Ginkgo biloba* Linné.

The figured specimen from Grand Coulee is entire, a condition frequently seen in leaves of the existing species. I have numerous specimens of the latter that exactly match the fossil.

*Juglans oregoniana* Lesquereux

*Juglans oregoniana* Lesquereux, Mus. Comp. Zool. Mem. 6: 35. *pl. 9. f. 10.* 1878.

Knowlton, U. S. Geol. Survey Bull. 204: 36. 1902.

*Rhus bendirei* Lesquereux, U. S. Natl. Mus. Proc. 11: 15. 1888 (according to Knowlton).

*Juglans hesperia* Knowlton, U. S. Geol. Surv. 18th Ann. Rept., pt. 3: 723. *pl. 99. f. 8.* 1898.

*Juglans egregia* Berry, Idem. Prof. Paper 170: 35. *pl. 11. f. 3.* 1931 (not Lesquereux).

<sup>3</sup> Depape, G. Compt. rendu Acad. Sci. 157: 957. 1913.

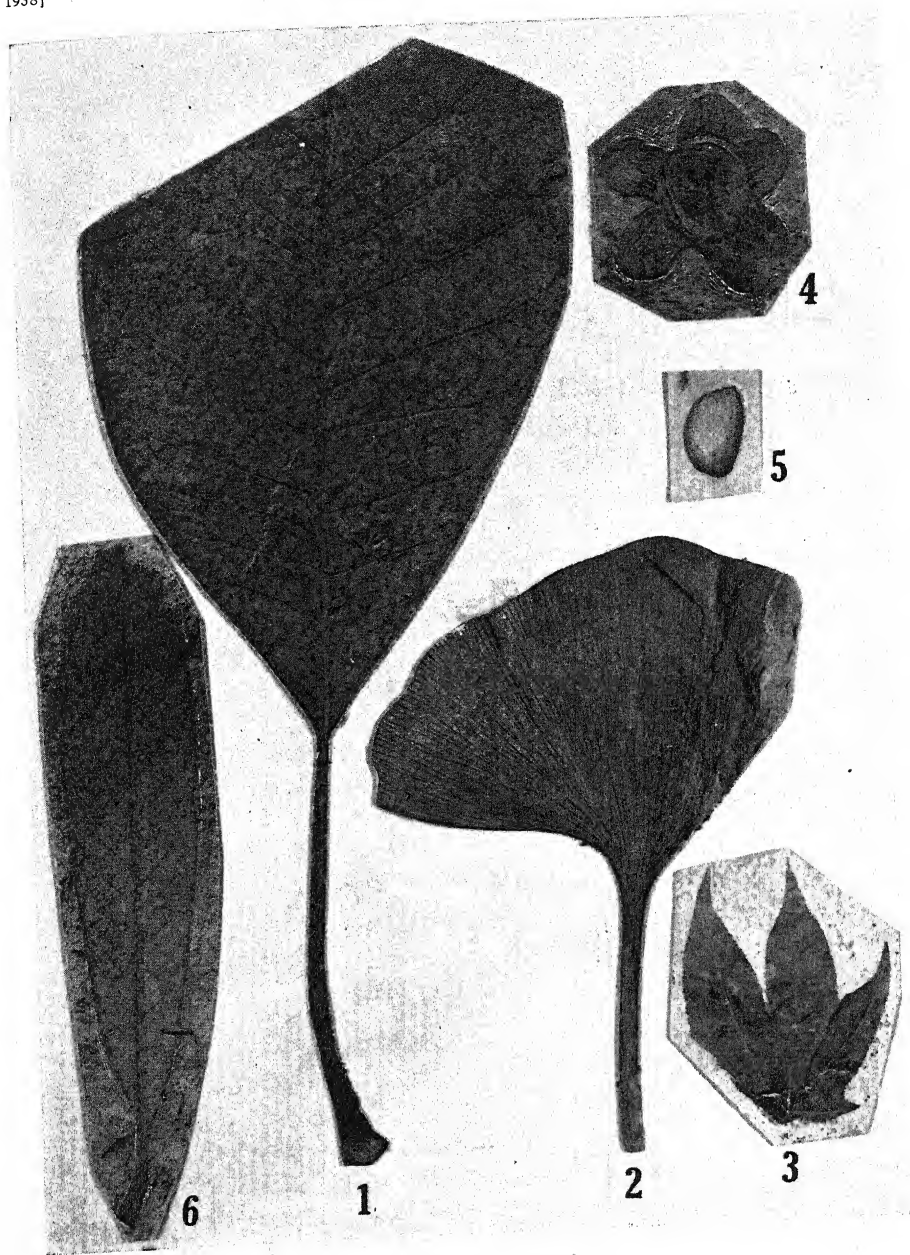


Fig. 1. *Magnolia spectabilis* Knowlton.  
Fig. 2. *Ginkgo adiantoides* (Unger) Heer.  
Fig. 3. *Liquidambar californicum* Lesq.  
Fig. 4. Calyx of *Diospyros Andersonae* Knowlton.  
Fig. 5. Seed of *Diospyros Andersonae* Knowlton.  
Fig. 6. *Castanopsis consimilis* (Newberry) Brooks.

I am not sure that *Juglans egregia* as defined by Lesquereux represents a botanic species distinct from *Juglans oregoniana* Lesquereux since both are very similar and highly variable but I have only included the leaves from Grand Coulee which I identified as the former. As thus conceived the species includes material from the Mascall formation of Oregon and the Payette formation of Idaho.

*Castanopsis consimilis* (Newberry) Brooks

Figure 6

*Quercus consimilis* Newberry, Proc. U. S. Natl. Mus. 4: 505. 1883: U. S. Geol. Survey Mon. 35: 71. pl. 43. f. 2-5, 7-10. 1898.  
*Castanopsis consimilis* Brooks, Ann. Carnegie Mus. 24: 285. pl. 6. f. 2; pl. 7. f. 3, 4; pl. 8. f. 1-5 etc., 1935.

Without implying complete agreement with Brooks' conclusions or the synonymy given by her for the above species, it would seem that a good case is made out for referring these leaves to *Castanopsis* instead of *Quercus*. I figure a typical specimen from Grand Coulee.

The genus, usually confused with other Fagaceae in the geological record, is represented by a single large tree (shrubby at high elevations) from southwestern Washington to southern California and by over a score of oriental species ranging from southern China to the eastern Himalayas and the Malay archipelago. The fossil is more like several of the Asiatic species than it is like the single surviving North American species.

*Quercus ursina* Knowlton

Figure 8

*Quercus ursina* Knowlton, U. S. Geol. Survey Bull. 204: p. 51. pl. 7. f. 2, 3. 1902. Berry, Idem. Prof. Paper 154: 246. 1929.

This species was based upon small 5 to 7 lobed leaves from the Mascall formation of the John Day basin in Oregon. It was subsequently detected in the Latah formation around Spokane, Washington and at both localities it was associated with the leaves identified as *Quercus Merriami* Knowlton. The leaf from the diatomaceous boulders at Grand Coulee which is here figured agrees very closely with Knowlton's types of *Quercus ursina*. It has 5 conical lobes prominently bristle-pointed and an extra bristle on one side near the tip. The base is less cuneate and more curved truncate, but is distinctly decurrent. *Quercus ursina* seems to have sufficient individuality to constitute a good botanical species. On the other hand its constant association with a great variety of highly variable oak leaves leads to a strong suspicion that it is simply a variant of one of these.

*Magnolia spectabilis* Knowlton

## Figure 1

*Magnolia spectabilis* Knowlton, U. S. Geol. Survey Mon. 32: 718. *pl.* 93. *f.* 1, 2. 1899.

*Magnolia dayana* Knowlton (not Cockerell) Idem., Prof. Paper 140: 41. *pl.* 24. *f.* 3. 1926.

*Magnolia* sp., Knowlton, Idem., *pl.* 27. *f.* 1.

The fine specimen from the brown sandy clay at Grand Coulee is identical with the material from the Latah formation at Spokane which Knowlton referred to *Magnolia dayana* Cockerell, a species from Chalk Bluff, California, and which I am sure is not that species.

The specimen from Spokane which Knowlton described as *Magnolia* sp. is, I believe, a variant of this same species. All of these appear to represent *Magnolia spectabilis* described originally from the supposed Miocene of Yellowstone Park. It would perhaps be useful to recharacterize this species which may be done in the following terms: Leaves prevaillingly large, elliptical-lanceolate, with a cuneate base and an abruptly pointed, usually not extended tip. Margins entire, usually evenly rounded but sometimes slightly undulate. The texture is not thick and leathery as Knowlton stated or as is found in the modern American evergreen *Magnolia foetida* Sargent but, as near as I can make out was fairly thin and stiff and might merit the term subcoriaceous. Length up to 20 centimeters. Maximum width up to 8.25 centimeters.

The petiole is very long and stout, curved, and enlarged at the base. Usually not preserved, it is complete in the Grand Coulee specimen and is about 6.5 centimeters in length, which is much longer than in most species of *Magnolia*. The midvein is stout and prominent. The secondaries are stout and prominent, 12 to 20 mostly alternate pairs, diverging from the midvein at angles of between 50 and 75°, generally rather straight proximad, becoming curved distad and eventually camptodrome. Tertiaries usually well marked comprising looped marginals and internal percurrent or forked veins at right angles to the secondaries and near the midvein subparallel with the secondaries both fading into an open more or less quadrangular areolation.

Knowlton thought that this species was an evergreen and this is possible although I can find no conclusive proof of this. He compared it with the living *Magnolia foetida* but it is less thick, less elliptical and has a longer petiole. It is more like the narrower leaves of the existing eastern Asiatic *Magnolia obovata* Thunberg which again has a much shorter petiole. Some of the forms from the Latah formation which have been referred to *Laurus*

*grandis* Lesquereux, as for example Knowlton's plate 24, figure 1, are certainly very similar to what is here called *Magnolia spectabilis* and I am not at all sure that they should not be transferred to the latter species. On the other hand specimens from the Latah which I have referred to *Laurus grandis*, as for example my plate 58, figure 3 appear to me to be lauraceous and quite distinct from *Magnolia*.

I have tentatively identified *Magnolia Inglefieldi* Heer from Grand Coulee and it is interesting to note that Knowlton compared *Magnolia spectabilis* with that species. The numerous specimens from the Arctic which Heer identified and figured as *Magnolia Inglefieldi*, if correct, show a wide range in size and form, and it is quite possible that the two magnolias from Grand Coulee represent the variants of a single botanical species.

*Magnolia Inglefieldi* Heer (?)

*Magnolia Inglefieldi* Heer, Fl. Foss. Arct. 1: 120. pl. 3. f. 5c; pl. 16. f. 5, 6, 8b; pl. 18. f. 1-3. 1868: Idem., 2: 478. pl. 44. f. 5b; pl. 51. 1871: Idem., 7: 121. pl. 69. f. 1; pl. 85. f. 3; pl. 86. f. 9. 1883.

Lesquereux, U. S. Natl. Museum Proc., 11: 13. 1888.

Knowlton, U. S. Geol. Survey Bull. 204: 58. 1902.

*Magnolia Inglefieldi* was described by Heer in 1868 from a large number of fragmentary specimens collected by Capt. Inglefield at Atanekerdluk in West Greenland. Additional specimens, including the cones, were figured in 1871 from collections made by Whymper. Additional specimens were figured in 1883 and altogether the species was recorded from five localities: Atanekerdluk, Ujararsusuk, Kudliset, Naujat and Asakak. These leaves show a considerable amount of variation and it is by no means certain that they all belong to a single species.

The one incomplete specimen and its counterpart from Grand Coulee is more like this species than any other that has been described, and is especially close to the specimen from Naujat, West Greenland, figured by Heer on plate 85 of the 7th volume of his *Flora Fossilis Arctica*.

Knowlton quotes Lesquereux for its identification in the Mascall beds of the John Day Basin in Oregon, but it is not contained in any of the collections except the early one made by Capt. Bendire and this material has never been figured so that it is impossible to say whether it is like the present specimens or some of Heer's smaller leaves. It is not unlike the modern *Magnolia acuminata* Linné, a mountain slope and stream bank type from western N.Y., southern Ontario, and southern Illinois to Kentucky, Tennessee, Alabama, Arkansas, and Mississippi. Most abundant and largest in mountain valleys of Tennessee and the Carolinas.



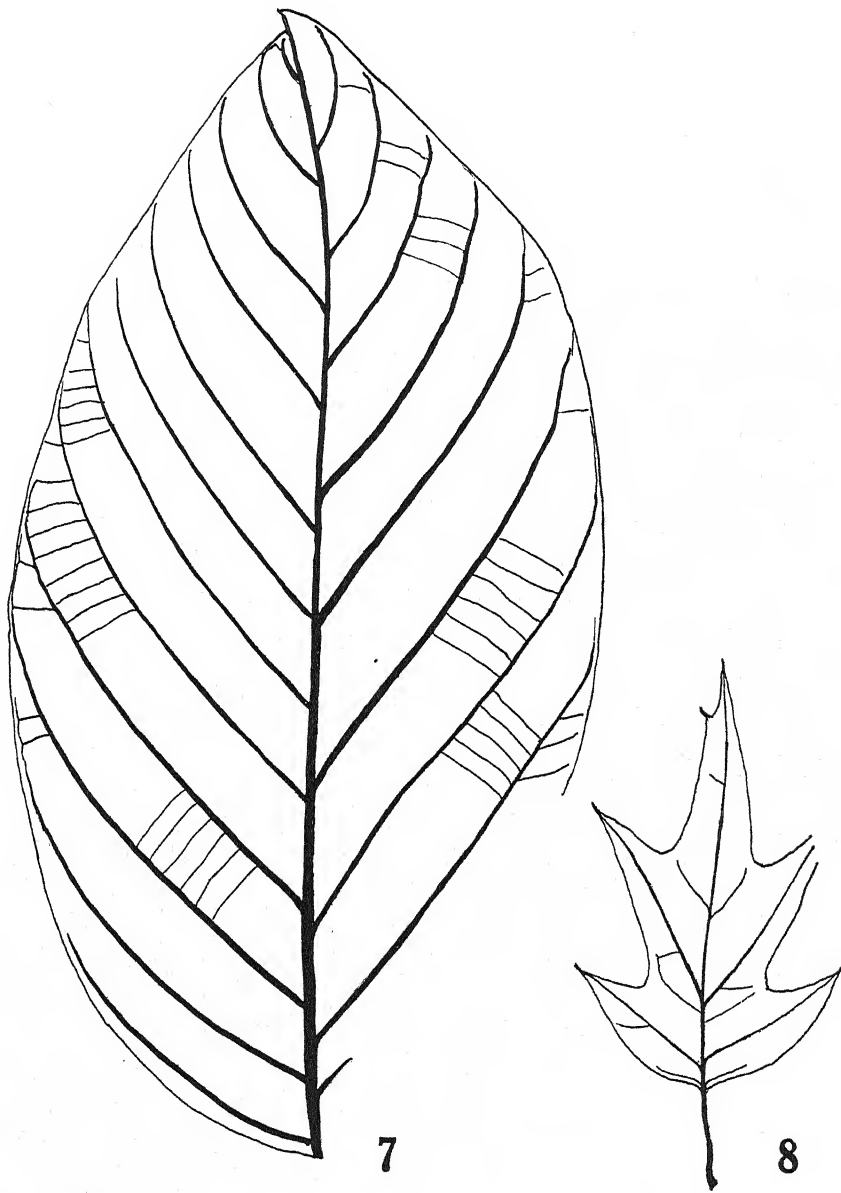


Fig. 7. *Cornus Becki* Berry, n. sp.  
Fig. 8. *Quercus ursina* Knowlton.

In shape and size and areolation it is very close to *Magnolia obovata* Thunberg (*M. hypoleuca* Sieb. & Zucc.) of Japan which, however, usually has the secondaries somewhat more closely spaced. This species occurs in the Pleistocene of Shiobara, Prov. Shimotsuke, Japan (Endo).

It is quite possible that what Knowlton<sup>4</sup> called *Magnolia culveri* from the supposed Miocene of Yellowstone Park should be referred to this species.

*Liquidambar californicum* Lesquereux, emended

Figure 3

*Liquidambar californicum* Lesquereux, Harvard Coll. Mus. Comp. Zoology Mem. vol. 6<sup>2</sup>: 14. pl. 6. f. 7c; pl. 7. f. 3, 6. 1878.

Chaney, Walker Mus. Contr., 2<sup>5</sup>: 174. 1920.

Berry, U. S. Geol. Survey Prof. Paper 154: 250. 1929.

*Liquidambar europaeum* Lesquereux, U. S. Geol. Survey Terr. Rept., vol. 8 (Cretaceous and Tertiary floras) 159. pl. 32. f. 1. 1883.

*Liquidambar pachyphyllum* Knowlton, U. S. Geol. Survey Bull. 204: 63. pl. 9. f. 1. 1902; U. S. Geol. Survey Prof. Paper 140: 42. pl. 22. f. 7; pl. 29. f. 1. 1926.

Chaney, Walker Mus. Contr. 2<sup>5</sup>: 174. pl. 15. f. 2, 3. 1920.

A few years ago I suggested that there was but a single Miocene species of *Liquidambar* in the western United States. This was based upon the well known variation of the leaves of the modern species in size, relative proportions and degree of lobation. It may indeed be doubted if the Miocene species can be distinguished from the existing species by its foliar characters.

In my original account<sup>5</sup> of the flora from Grand Coulee this species was not specifically recorded since the only traces of *Liquidambar* found were the fruits, which were found in both the brownish clays and in the diatomaceous boulders. These were not merged with the leaf species although it seemed obvious that both leaves and fruits belonged to a single botanical species. I also commented on the abundance of fruits at Grand Coulee and the absence of leaves. This deficiency has now been remedied since in the Beck collection from the brownish clays there is a medium sized three-lobed leaf and a small, incipiently five-lobed leaf. Since *Liquidambar* leaves are easily macerated it seems certain that the parent tree was not far removed from the place of fossilization and that the abundant fruits need not have been brought into the basin of deposition from any distance.

The smaller of the two leaves is figured in the present paper.

<sup>4</sup> Knowlton, F. H., U. S. Geol. Survey Mon. 32: 720. pl. 92. f. 5. 1899.

<sup>5</sup> Berry, E. W., U. S. Geol. Survey Prof. Paper 170 C, 1931.

**Cornus Becki** Berry n. sp.

## Figure 7

Leaves of relatively large size, ovate in outline, slightly inequilateral, with the end of the midvein slightly recurved and the tip of the lamina slightly conduplicate. Margin entire. Length about 15 centimeters. Maximum width about 8 centimeters. Petiole not preserved. Midvein relatively narrow but prominent, usually faintly sigmoidally curved. Secondaries thin, prominent, 9 to 12 pairs; they diverge from the midvein at acute angles, are unequally spaced but subparallel, ascending in sweeping curves, terminating in camptodrome arches so close to the margins as to usually be indistinguishable. Tertiaries thin, mostly percurrent. Areolation indistinct. Named for the collector, George F. Beck.

There are a number of genera with leaves similar to these. The general shape and secondary pattern is not unlike *Diospyros* which is represented by splendid large fruits at Grand Coulee, but the tertiary venation is not that of *Diospyros*. Leaves similar to these are also often referred to *Ficus*, especially if they occur in the earlier Tertiary, and there is considerable resemblance to what Lesquereux called *Magnolia californica*,<sup>6</sup> but again there are obvious differences in ascent and endings of secondaries and the character of the tertiaries.

Leaves of this sort from the older Tertiary are frequently referred to *Rhamnus* or *Rhamnites*, but I know of no Miocene or Recent species that are especially similar.

The totality of observed features are distinctly those of *Cornus* and the leaves of the existing western *Cornus Nuttallii* Audubon are not especially different except that they are usually considerably smaller. Our eastern arborescent dogwood, *Cornus florida* Linné although normally with smaller leaves does occasionally produce leaves as large as the fossil and these are scarcely distinguishable from it.

The geological history of *Cornus* goes back to the Upper Cretaceous. There are four species known from the western Miocene, two from California, one from Yellowstone Park and the fourth from the Latah formation at Spokane. The last, *Cornus acuminata* Berry is conspicuously different from *Cornus Becki*, being a narrow acuminate leaf like those of the living *Cornus canadensis* Linné.

**Diospyros Andersonae** Knowlton

## Figures, 4, 5

*Diospyros Andersonae* Knowlton, U. S. Geol. Survey Prof. Paper 140: 46. *pl.* 27. *f.* 6. 1926.

<sup>6</sup> Lesquereux, L., Mus. Comp. Zool. Mem. 6: 25. *pl.* 6. *f.* 6, 7. 1878.

This fine calyx was described by Knowlton from a specimen found in the Latah formation exposed in a cut on the Spokane, Portland and Seattle Railway in Spokane. It<sup>a</sup> was naturally compared with the calyx of the living persimmon of southeastern North America—*Diospyros virginiana* Linné from which it differed in merely minor details. It was evidently not often fossilized in the Latah sediments as I have not seen it in the large amount of material that I have studied from the Spokane region, but this can not be taken to indicate that the parent tree was rare, since the Latah contains large numbers of leaves of a *Diospyros* which I have called *Diospyros princetoniana* Cockerell<sup>7</sup> and which presumably represents the same botanical species as the calyx.

In the diatomaceous clay from Grand Coulee there is a very fine specimen of a persimmon calyx, which can hardly represent other than this same species. It is slightly larger than the type but is identical with it in general features, texture, etc., differing from it in having five instead of the normal four calyx-lobes. The number of these lobes can not be considered a specific character since five occur occasionally in both our existing American and in Asiatic forms.

Although the present fossil is very similar to the calyx of *Diospyros virginiana* this similarity does not impress me as strongly as it did Knowlton and in particular the shape and venation of the lobes is more similar to the Asiatic cultivated form.

Of the greatest interest is the occurrence of an unmistakable seed of *Diospyros* about one-quarter of an inch away from the calyx and at a level about one-eighth of an inch removed from it. This seed is almost exactly the size, shape and has the papillated surface of the seeds of *Diospyros virginiana* and probably came from the same fruit that furnished the calyx. Under the circumstances it seems to me that it would be absurd not to consider the seed as belonging to the same species.

<sup>7</sup> Berry, E. W., U. S. Geol. Survey Prof. Paper 154: 263. *pl.* 59. *f.* 6; *pl.* 60. *f.* 1-3. 1929.

### Studies in the Ericales III.

#### The genus *Leiophyllum*

W. H. CAMP

During the identification of certain specimens of *Leiophyllum*<sup>1</sup> collected by the writer in New Jersey in 1933 and the southern Appalachians in 1936, a critical review of this eastern North American genus seemed advisable. It was soon apparent in the study of the three species (*L. buxifolium*, *L. Lyoni*, and *L. Hugeri*) which are sometimes recognized as those of which the genus is composed, that certain of the specific distinctions which had been emphasized in the past were of little phylogenetic significance and of still less taxonomic convenience.

The distribution of the genus is interesting, for it ranges from certain of the higher summits of the Smokies and the Blue Ridge in Tennessee and North Carolina, across the states of North and South Carolina (several disjunct stations) to the coast, where it is known from the region near Cape Fear. From here there is a jump of nearly 450 miles to the next nearest station in the pine-barrens of New Jersey where it is fairly common, and in local areas even abundant.

Much has been written concerning the distribution of genera and species limited to the southern Appalachians and the coastal plain in the region of the New Jersey pine-barrens. It, therefore, will be unnecessary to review the literature at this time. Since the genus under consideration—as its eight to twelve sister genera in the Phyllodoceae of the Ericaceae—is obviously a remnant of the Late Mesozoic and Early Tertiary dispersal of the heath family, it will be essential only to outline the probable distribution of the genus *Leiophyllum* in the Tertiary.

It is becoming increasingly doubtful in the mind of the writer whether many of the genera or species endemic on the peaks of the southern Appalachians really originated there. It is more likely that their evolution took place either in the earlier highlands slightly to the southeast, or in other regions, and that their occurrence on the backbone of the present mountain system is to be explained on the basis of relic colonies of a once more widely dispersed group. It is a truism that endemism is common on

<sup>1</sup> *Leiophyllum* (Pers.) Hedw. fil. Gen. 313. 1806, is to be preferred over *Dendrium* Desv. Jour. de Bot. II. 1: 36. 1813. It is not preoccupied by *Leiophyllum* Ehrh. 1789, which is without description and invalid and admitted by Ehrhart himself to be without standing as a generic name. Points in the bibliography of this genus have been discussed by Barnhart (Rhodora, 22: 180-182. 1920) and Fernald (Rhodora, 29: 225-227. 1927). Dr. Barnhart and the present writer, on the basis of copies of the "Journal" in our own library, are unable to agree with Professor Fernald on his citation for *Dendrium*, maintaining that the one given above is the more correct. In any event, we all agree that *Leiophyllum* is the correct name.

many mountain systems, but this fact does not necessarily lead to the conclusion that "mountains make species." It is the contention of the writer that mountains capture aggressive genetic biotypes and because of their isolation and variations in altitude and habitat, tend to conserve these biotypes during subsequent climatic and floristic disturbances. A relatively small change in elevation or climate is sufficient to change the whole floristic aspect of a piedmont or lowland region and eliminate many of the species represented in it, whereas the same variation might require the plants on a favorably situated and contiguous mountain area to migrate only a few hundred feet in altitude to come to rest in habitats suitable for their preservation.

It seems, therefore, to the writer that, in the Early Tertiary, the genus *Leiophyllum* was more widely distributed than at present on what is now the piedmont of the southern Appalachians and that this region was the home of the basic species. During the climatic changes and orogeny of the Tertiary, two easy avenues of migration were open. One was into the mountain systems to the northwest undergoing a cycle of secondary elevations; the other was to the coastal plain. Both of these migrations evidently took place.

The basic species of *Leiophyllum* apparently was a plant sometimes in excess of a meter in height with mostly alternate, longish leaves inclined to be apically obtuse to acute, or at least apiculate, and bearing stalked glands on its flower and fruit pedicels. The biotype which originated in, or possibly near, and later migrated onto the present higher mountains, differed in being somewhat more spreading, and particularly in having its leaves mostly opposite, more oval, or sometimes suborbicular, apically rounded and rarely apiculate. The early range of this mountain form probably was reduced by the climatic changes of the Late Pliocene and the Pleistocene.

When the basic species migrated to the then periodically broader coastal plain, its biotypes found there an environment which was remarkably uniform for a stretch of almost 700 miles from the Carolinas to the deep Tertiary valley of the Hudson River. This rather wide and probably common distribution of the plant in question was destined to be comparatively short-lived, for the series of submergences of the coastal plain during the Middle and Late Tertiary apparently eliminated the plant between Cape Fear and Cape May. During one of these later submergences (the Pensauken?) the present pine-barren region of New Jersey, for a time, was probably isolated from the mainland. It was the incomplete submergence of this area, together with its peculiar soil conditions, which permitted so many of the southeastern coastal plain species and those of peculiar habits which had wandered there from the piedmont and those of mountains, to find refuge from a too severe competition and thus escape elimination.



The type of the genus [*Leiophyllum buxifolium* (Berg.) Ell.] undoubtedly was collected in New Jersey and for a long time the material from this region has been supposed to be easily differentiated from the mountain forms by the absence of glandular hairs on its flower and fruit pedicels and in part on leaf arrangement. (It is the opinion of the writer that other of the flower and fruit characters often used are of too fluctuating a character to be reliable.) However, a careful examination of material from the New Jersey localities revealed, in certain areas at least, that the pedicels of a considerable number of the plants bore gland-hairs. At the same time it was noted that the bracts, and particularly the pedicels of the eglandular material were somewhat more glaucescent than the same parts of those plants whose pedicels were glandular. These plants with gland-bearing pedicels were obviously very closely related to the material found eastwards from the mountains and on the coast of North Carolina, all of which undoubtedly represent remnants of the once more widely dispersed basic species.

It is thought that the eglandular material from New Jersey represents a mutant form which was abundant on the relatively small island off the coast during the Pensauken (?) submergence; a form so common in that peculiar area that even to the present it constitutes a large proportion of the specimens seen. A recently studied collection from Springville (near Darlington), South Carolina (P. H. Rogers, April 10, 1912), contained a little material approaching the eglandular form found in New Jersey. It is therefore possible that both forms might have been present throughout the entire coastal plain range of the genus. At least, they should not be thought of as being distinct species.

The problem of matching names and specimens is not an easy one. The abundant material from New Jersey, the pedicels of which are eglandular, is consonant without ideas of *Leiophyllum buxifolium* var. *typicum* C. K. Schneider. The opposite-leaved material from the mountain summits is harder to place. The oldest name which is available is *Leiophyllum Lyoni* Sweet. The original description, however, consists of a single word: "spreading". In the absence of a type specimen, this inadequate description gives us considerable latitude and it has been the custom of some of the more recent writers to assign this name only to the occasional prostrate forms found on certain of the mountain summits. A study of these forms indicates that they are not separable from the rest of the high-mountain material and are probably the result of environment. *L. Lyoni*, therefore, should be used for the more common mountain plant.

During the course of this investigation it was found that most of the collections assigned to *Dendrium Hugerii* Small, 1901 (*L. Hugerii* Schneider, 1903. *L. buxifolium* var. *Hugerii* Schneider, 1911.) were not conspecific with the type specimen, but belonged to the group of plants defined by the

present writer as *L. Lyoni*. The reduction of *Hugeri* to a variety was, for Schneider, a blind, but fortunate decision. If one may judge by the specimens seen from foreign gardens, his further statement that *Hugeri* is the common form in cultivation in Europe, clearly indicates that he was certainly less aware of its correct relationships than the original author of the species and surely ignorant of the type specimen and the material from the piedmont.

The type of *Hugeri* is unfortunate for, although it belongs with the material forming the basic species, it is an extreme specimen and may in part be contaminated with the heredity of *Lyoni*. While it must remain as the "nomenclatorial type" it is not to be regarded as biologically typical. It is thought best, however, rather than inject a new name into our taxonomic literature (since this particular specimen could be included as an extreme) to retain *Hugeri* as the name for the fundamental biotype of the genus. Unfortunately, because of present rules, the basic entity must take subordinate nomenclatorial rank for I am unable to discern more than a varietal difference between *buxifolium* and *Hugeri*. Because of its differences in phyllotaxy<sup>2</sup> and leaf form from *L. buxifolium* vars. *typicum* and *Hugeri*, the writer maintains *L. Lyoni* as a distinct species.

It is to be admitted that, during the course of this study, various minor biotypes based on pedicellary puberulence, leaf form and flower structure were observed, some of them with remarkably stable characters which obviously were the result of local endemism. I feel, however, that the addition of a whole series of new subspecific names to our North American ericaceous literature is at present neither necessary nor advisable. The picture of the genus presented here seems, in my opinion, to be taxonomically sufficient to take care of the known material and in addition gives a working hypothesis of the origin and migrations of the various recognized entities in the genus.

The following key and list of localities, with specimens cited fully only in the case of var. *Hugeri*, summarizes the writer's present knowledge of the genus.

#### KEY TO THE GENUS *LEIOPHYLLUM*

- Leaves mostly *alternate*, longish and apiculate.
  - Pedicels eglandular..... *L. buxifolium* var. *typicum*.
  - Pedicels glandular..... *L. buxifolium* var. *Hugeri*.
- Leaves mostly *opposite*, elongate-oval to orbicular and apically rounded, rarely apiculate.....
  - ..... *L. Lyoni*.

<sup>2</sup> In the Ericaceae, the occurrence of opposite leaves is a departure from the normal and points to evolutionary specialization. This particular character is not a completely fixed habit in *L. Lyoni* and in rapidly growing stems the phyllotaxy may occasionally revert to alternate, indicating its close relationship with and derivation from var. *Hugeri*. Conversely, dwarfed and stunted branches of *buxifolium* vars., may sometimes bear nearly opposite leaves.



LEIOPHYLLUM BUXIFOLIUM var. TYPICUM C. K. Schneider.

NEW JERSEY. ATLANTIC: Hammonton; Landisville. BURLINGTON: Atsion; Batsto; Chatsworth; Marlton; New Lisbon; Quaker Bridge; Woodmansie. CAMDEN: Waterford. MONMOUTH: Freehold. OCEAN: Forked River; Lakehurst; Manchester; Toms River; Waretown; Whitesville; between Warren Grove and Symmes Place.

LEIOPHYLLUM BUXIFOLIUM var. HUGERI (Small) C. K. Schneider.

SOUTH CAROLINA. DARLINGTON: Springville (near Darlington) along sandy banks and sand hills of Black Creek, *P. H. Rogers* Apr. 10, 1912 (in part tending toward var. *typicum*); Darlington, *T. G. Harbison* 18 Dec. 18, 1918; *ibid.* *T. G. Harbison* 33 Nov. 22, 1919. PICKENS: Table Mt., *J. K. Small* Aug. 1896 (Type); *ibid.* *Buckley* (Ex. Herb. Geo. Thurber). This specimen lying in the Gray Herbarium agrees almost exactly with the type.

NORTH CAROLINA. AVERY: Cañon of Linville River, *John McRae* Sept. 1896. (Mitchell Co. on label). BRUNSWICK: Wilmington to Southport, *W. C. Coker* Apr. 6, 1918; 12 mi. from Southport, *W. C. Coker and party* May 15, 1926; north of Southport, *E. B. Bartram* Jan. 28, 1922; Orton Plantation, 15 mi. n.e. of Southport, *A. C. Matthews* Apr. 9, 1935; 4 mi. e. of Bolivia, *J. M. Fogg, Jr.* 5492 Apr. 16, 1933; without locality, *M. A. Curtis*. BURKE: Wiseman's View, Linville Mts. *Alexander, Everett and Pearson* Oct. 10, 1933; Ervin's View, Linville Falls, *Anne R. Clement* June 17, 1934; *ibid.* "Irwin's View," above Linville Falls, *W. C. Coker* Sept. 10, 1927. CALDWELL: Hibriten Mt., near Lenoir, *A. M. Huger* Sept. 1896. CUMBERLAND: Cultivated at Red Springs but taken from plants said to be "plentiful" near Fayetteville, *Mary Vardelle* Apr. 1923. NEW HAMPSHIRE: "Cape Fear" near Wilmington, *E. J. Palmer* 39825 Apr. 12, 1923. STOKES: Piedmont Springs, *L. Barksdale* Apr. 29, 1934; Cascade Falls near Piedmont Springs, *H. R. Totten* May 12, 1929.

NEW JERSEY. ATLANTIC: Egg Harbor, *J. B. Brinton* May 18, 1890. BURLINGTON: Chatsworth, *E. H. Eames* June 14, 1894; *ibid.* *J. T. P. Byhouwer* and *C. E. Kobuski* 80 May 25, 1928; Pemberton, *L. H. Lighthipe* May 27, 1884. CAMDEN: near Albion, *U. B. Meredith* June 7, 1924; Sumner, *A. Haines* 311 June 2, 1906; without locality, *C. F. Parker* June 2, 1867. OCEAN: without locality, *P. Birdsall* May 15, 1891; Forked River, *J. R. Churchill* May 27, 1891 (in part); Manchester, *N. L. Britton* Aug. 28, 1879; *ibid.* *J. W. Chickering, Jr.* July 19, 1873; *ibid.* (without collector) "Ex Herb. Torr." May 16, 1870; Toms River, *P. Wilson* July 3-5, 1916; *ibid.* *J. I. Northrop* May 30, 1887; *ibid.* *A. B. Clute* May 27, 1888; *ibid.* *W. W. Eggleston* May 30, 1907.

*LEIOPHYLLUM LYONI* Sweet.

TENNESSEE: SEVIER: Great Smoky Mts. Nat'l. Park, Mt. Leconte; The Chimneys.

TENNESSEE and NORTH CAROLINA. Line between CARTER Co., TENN. and MITCHELL Co., N. C.; Roan Mt.

NORTH CAROLINA. AVERY: Northeast of Linville; Banners Elk. Line between AVERY and WATAUGA: Grandfather Mt. BURKE: Table Rock Mt. Line between HAYWOOD and TRANSYLVANIA: Devil's Court House. JACKSON: Whitesides Mt.; Sapphire. MACON: near Highlands; *ibid.* top of Satulah Mt.; *ibid.* Sunset Rocks; Mt. Whiteside; "Crest of the Blue Ridge." McDOWELL: Shortoff Mt., near Marion.

During the course of this study the writer examined all available specimens of the genus in the Herbarium of the University of North Carolina, Herbarium of the Arnold Arboretum, Gray Herbarium, U. S. National Herbarium and the Herbarium of the New York Botanical Garden.

THE NEW YORK BOTANICAL GARDEN

## Studies in Onagraceae XI. A revision of the genus *Gaura*

PHILIP A. MUNZ

(WITH EIGHTEEN FIGURES)

During the past several years I have had opportunity to visit much of the area in which *Gaura* is distributed and to work in many of the herbaria in which types are deposited. Among these herbaria are those at British Museum (BM), Bossier Herbarium (Boiss), Delessert Herbarium (Del), Edinburg (Edin), Kew(K), and Paris (P). In addition to types above mentioned, I have had for study the material at Gray Herbarium (G), Herbarium of New York Botanical Garden (NY), Pomona College (P), and at the United States National Herbarium (US). To all those in charge of the above institutions I gladly express my gratitude. I wish particularly to acknowledge my indebtedness to Mr. V. L. Cory of Sonora, Texas, whose abundant collections of Onagraceae in that state have been most helpful to me.

In this paper I am using the word *Gaura* in the same sense as that of Bentham and Hooker, Rothrock, and Engler & Prantl, namely excluding *Stenosiphon*, *Heterogaura*, and *Gonglyocarpus*. For the sake of space, I shall not here present any opinions on phylogeny and relationship, which are being reserved for a future paper on the whole family.

### GAURA L.

*Gaura*, L., Nov. pl. Gen., 47, 1751; Amoen. Acad. 3: 26. 1756. Endlicher: Genera Pl., no. 6131, 1836-'40. DeCandolle, Prodrum 3: 44. 1828. Rothrock, J. T., Proc. Amer. Acad. 6: 349. 1864. Benth. & Hooker, Genera Pl. 1: 792. 1867. Raimann in Engler & Prantl, Die Nat. Pflanzenfam. III, 7: 218. 1898.

*Gauridium* Spach, Hist. Vég. Phan. 4: 379. 1835.

*Schizorcarya* Spach, Ann. Sci. Nat. Sér. II, 4: 170, 283. 1835.

Flowers white to pink (yellow in one species), in spicate to subcapitate racemes, more or less symmetrical, usually irregular, 4-merous, sometimes 3-merous. Hypanthium obconic or cylindrical. Stamens twice as many as the petals, declined, all fertile, each usually with a scale at the base of the filament. Stigma more or less deeply 4- (3-) lobed, and provided at the base with a cuplike indusium. Ovary 4- (3-) locular, or partition obsolete; ovules solitary or rarely 2 in the locules. Style filiform, deflexed. Fruit woody, small, 4- (3-) sided, indehiscent, sometimes 4- (3-) cleft apically, 4- (3-) seeded or 1-seeded by abortion. Annual or perennial herbs, rarely suffruticose.

Type species,—*G. biennis*. L.

#### KEY TO SPECIES

- A. Capsule sessile or nearly so, not narrowed into a pedicel-like base, except sometimes in *brachycarpa* and *gracilis*.

- B. Petals yellow, aging red, subequal, rhombic, 14–15 mm. long; hypanthium 25–35 mm. long; sepals 15–18 mm. long. Mexico. 1. *G. mutabilis*.<sup>1</sup>
- BB. Petals white to pink or red, in 2 pairs (1 more or less erect, the other spreading to the side); hypanthium 1–12 mm. long; sepals 1.5–15 mm. long.
- C. Flowers small; petals 1.5–2 mm. long; sepals 1.5–3 mm. long; anthers oval, 1 mm. long. 2. *G. parviflora*.
- CC. Flowers larger; petals 3–20 mm. long; sepals 4–15 mm. long; anthers oblong to linear, 2–5 mm. long (1 mm. in *angustifolia*).
- D. Fruit with rounded or obtuse angles, pubescent, more or less fusiform.
- E. Hypanthium 5–7 mm. long; fruit 4–7 mm. long. E. Texas & Okla. to Ia. & Atlantic coast. 3. *G. biennis*.
- EE. Hypanthium 8–12 mm. long; fruit 7–15 mm. long.
- F. Sepals 9–11 mm. long; petals 8–10 mm. long; filaments 8–10 mm. long. New Mex. & Colo. 4. *G. neomexicana*.
- FF. Sepals 6–7 mm. long; petals 5 mm. long; filaments 3–4 mm. long. W. Texas. 5. *G. macrocarpa*.
- DD. Fruit sharply angled.
- E. Sepals 12–15 mm. long; petals 12–20 mm. long; filaments 10–15 mm. long. S. E. Texas and adjacent La. & Mex. 6. *G. Lindheimeri*.
- EE. Sepals 4–10 (12) mm. long; petals 4–10 mm. long; filaments 3–7 mm. long.
- F. Fruit 3-angled; flowers 3-merous.
- G. Plant usually simple below, 6–18 dm. tall; petals 4–6 mm. long; fruit elliptic to ovoid, the faces not transversely wrinkled. Car. to Fla. & Ala. 7. *G. angustifolia*.
- GG. Plant usually branched from base, 2–6 dm. tall; petals 3–4 mm. long; fruit pyramidal, the faces transversely wrinkled. Okla. to Mex. 12. *G. tripetala*.
- FF. Fruit 4-angled; flowers 4-merous.
- G. Sepals 4–7 mm. long (sometimes 8 in *brachycarpa*.)
- H. Fruit pyramidal, tapering from base upward; anthers 2 mm. long. Texas to Mex. and Ariz.
- I. Sepals 4–5 mm. long; cauline leaves 1–3 mm. wide; wings of fruit not auricled at base. 10. *G. gracilis*.
- II. Sepals 6–7 (8) mm. long; cauline leaves 5–12 mm. wide; wings of fruit auricled at base. 11. *G. brachycarpa*.
- HH. Fruit ovoid to elliptic, somewhat narrowed at both ends; anthers 1 mm. long. Car. to Fla. and Ala. 7. *G. angustifolia*.
- GG. Sepals 8–10 (12) mm. long.
- H. Inflorescence canescent-strigulose to villous; anthers 2.5–3 (4) mm. long. 8. *G. filiformis*.
- HH. Inflorescence glabrous; anthers 4–5 mm. long. 9. *G. suffulta*.
- AA. Capsule narrowed into a distinct thick or slender stipe-like base.
- B. Stipe-like base of capsule very slender (almost filiform), the capsule-body being abruptly narrowed at base.
- C. Plant soft-villous with long hairs; stipe-like base of fruit 3–6 mm. long; petals 8 mm. long. Kansas to Texas & New Mex. 13. *G. villosa*.
- CC. Plant pubescent to glabrous; stipe-like base 1–3 mm. long; petals 4–6 mm. long. East of Mississippi River.
- D. Capsule obovoid-clavate, the stipe-like base mostly 1.5–3 mm. long. 14. *G. filipes*.

<sup>1</sup> For the species *G. mutabilis* I accept the section *Gauridium* (Spach) Endlicher, Gen. Pl. no. 6131. The other species I would include in the section *Eugaura* n. nom. with white to pink, somewhat irregular flowers.

- DD. Capsule elliptic to narrowly ovoid, the stipe-like base 0.5–1 mm. long.  
 7. *G. angustifolia*.
- BB. Stipe-like base of capsule stout, the capsule-body being more gradually narrowed at the base.
- C. Hypanthium and sepals with minute gland-tipped hairs; stipe-like base of fruit 1–1.5 mm. long; face of fruit transversely wrinkled. W. Texas to Ariz. 15. *G. Nealleyi*.
- CC. Hypanthium and sepals not glandular; stipe-like base of fruit 2–5 mm. long; face of fruit not transversely wrinkled.
- D. Hypanthium 2.5–4 mm. long; filaments 8–10 mm. long; fruit 5–9 mm. long, 1–1.5 mm. wide. Okla.-Mex. 16. *G. sinuata*.
- DD. Hypanthium 5–12 mm. long; filaments 3–6 mm. long.
- E. Fruit 1.5–2 mm. wide, 10–15 mm. long, narrowly fusiform, sometimes curved, ribbed but not angled. Western Texas and adjacent Mex. 5. *G. macrocarpa*.
- EE. Fruit mostly 2–3 mm. wide, the ovoid body 4-angled and rather rapidly narrowed basally into a terete obconic stipe.
- F. Sepals 10–13 mm. long; petals 7–8 mm. long; floral bracts lance-ovate, caducous. Texas to southern Mex. 17. *G. odorata*.
- FF. Sepals 5–9 mm. long; petals 3–6 mm. long; floral bract lanceolate to linear, mostly persistent. Alberta to central Mex. 18. *G. coccinea*.

## TREATMENT OF SPECIES

1. *GAURA MUTABILIS* Cav., Icon. 3: 30, pl. 258. 1795.

*Gauridium mutabile* Spach, Hist. Vég. Phan. 4: 380. 1935; Nouv. Ann. Mus. Paris (III) 4: 374. 1835. *Oenothera anomala* Curtis, Bot. Mag., pl. 388, 1797. *Gaura mollis* HBK., Nov. Gen. et Sp. 6: 93, pl. 529. 1823. *Gauridium molle* Spach, Hist., 1. c. *G. Kunthii* Spach, Nouv. Ann., 1. c. 375. *Gaura oenotherifolia* Zucc., in Roemer, Collect., 140, 1809. *G. canescens* Hort., ex Ser. in DC., Prodr. 3: 45. 1828. *Oenothera Héribaudi* Léveillé, Fedde Repert. Nov. Sp. 8: 280. 1910.

Perennial herb from heavy rather woody caudex, bushy, much branched throughout, 3–6 dm. high, short- and soft-villous throughout; leaves well distributed in lower half or two-thirds of plant, the basal ones oblanceolate to spatulate in outline, 4–8 cm. long, 8–20 mm. wide, sinuate-dentate especially on the winged petiole; cauline leaves lanceolate to ovate, acute, sinuate-denticulate, almost or quite sessile, gradually reduced up the stem, mostly 2–4 cm. long and 5–20 mm. wide; inflorescence with deciduous lance-ovate bracts 3–4 mm. long, not peduncled, elongating in fruit to 1–2 dm., spicate; buds erect; flowers opening in evening; hypanthium slender, pubescent without 25–35 mm. long, often somewhat reddish, short-retrorse-pubescent within; sepals with some red, pubescent, 15–18 mm. long, lanceolate, more or less adherent in anthesis, without free tips; petals rhomboid, yellow in anthesis, orange-red in age, quite equal, 14–15 mm. long; stamens yellowish, slightly unequal, equalling or exceeding petals, the filaments slightly flattened, glabrous, with no evident basal scale; anthers linear, 4–5 mm. long; style exerted well beyond stamens, 4–6 cm. long from summit of ovary, retrorse-pubescent at very base; stigma-lobes linear, 2–3 mm. long; capsules fusiform, sometimes

curved, 4-nerved and obtusely 4-angled, usually pubescent, 7–14 mm. long, 2–4 mm. thick, 1-few-seeded; seeds flattened, brown, overlapping smooth.

Type locality, "Habitat in Nova-Hispania." Well distributed in Mexico. Representative material: without locality, Jardin du Luxembourg, in 1822, "graines envoyées par Lagasca" (K photo at P); "*G. mutabilis* m. Lagasca, 1806," Prodrômus Herb. (Del); "*G. oenotheriflora* Zucc. m. Balbis, 1808," Prodrômus Herb. (Del); *G. mollis*, Herb. Humboldt & Bonpland (Paris). CHIHUAHUA: Chihuahua, *Pringle* 1125 (G, US); between Cusihiuriachic & Guerrero, *Pringle* 1244 in part (NY). DURANGO: Otinapa, *Palmer* 460 (G, US); El Salto, *Nelson* 4570 (P, US). GUANAJUATO: Guanajuato, *Dugès* 6 (G), 303 (G). DISTRITO FEDERAL: Pedrigal, *Pringle* 6661 (G, NY, US); Santa Fé, *Rose & Painter* 6504 (G, NY, US), *Borgeau* 296 (G, US). HIDALGO: Marquez, *Pringle* 7635 (P, photo US). PUEBLA: San Luis Tultitlanapa, *Purpus* 3388 (G, NY, US); Bord del l'Alsesécon, *Nicolas* in 1909, *Oe. Héribaudi* (Del, US, photo at P), in 1910 (Edin, US). OAXACA: without locality, *Andrieux* (G, Del).

The specimens cited above are pubescent in the inflorescence, while the following are characterized by a glabrous inflorescence and may be designated as forma **glabra** n. nom. (synonym, *G. grandiflora* Rose, Contrib. U. S. Nat. Herb. 12: 293. 1909): CHIHUAHUA: between Cusihiuriachic & Guerrero, *Pringle* 1244 in part (G, NY, US). DURANGO: Durango, *Palmer* 270 (G, US) and (NY in part); Papasquiario, *Nelson* 4671, type *grandiflora* (US). The lack of pubescence is not definitely enough correlated either with distribution or any morphological characters to warrant more than such rank.

There might be some argument for recognizing the genus *Gauridium*, since this species is the only yellow-flowered one and the base of the filaments lacks a scale. But such scale is not found in *Guara parviflora* and color alone with perhaps a more regular flower hardly seems to warrant generic rank.

2. GAURA PARVIFLORA Dougl., ex. Hooker, Fl. Bor. Am. 1: 208. 1834.

Apparently a biennial or winter annual, from 2–20 (30) dm. tall, erect, rather simple below, simple or more commonly freely and widely branched above, soft-villous almost throughout with spreading white hairs, also with shorter glandular ones; leaves soft-pubescent, simple, alternate; rosette leaves typically broadly oblanceolate, 5–15 cm. long, 1–3 cm. wide. remotely sinuate-denticulate, the blade proper gradually narrowed into winged petioles; cauline leaves gradually reduced upward, almost or quite sessile, entire or remotely sinuate-denticulate, lanceovate to lanceolate, acuminate to acute, 3–10 cm.



long, 1-2.5 (3.5) cm. wide; bracts lance-linear, 2-5 mm. long, caducous; flowers opening in evening, in terminal slender spikes which usually nod at tips and become 1-3 dm. long; hypanthium 1.5-3 mm. long, slender, glabrous to short-pubescent without, pubescent within; sepals greenish to reddish, 1.5-3 mm. long, oblong-lanceolate, reflexed separately in anthesis, glabrous to puberulent; petals spatulate, mostly pink or rose, 1.5-2 mm. long, erect, slightly clawed; stamens slightly shorter than sepals, basal scale obsolete; filaments rose, flattened, the episepalous slightly longer than epipetalous; style reddish, projecting about as far as sepal-tips, usually pubescent on basal portion (inside hypanthium); anthers reddish, ca. 1 mm. long, oval versatile; stigma with 4 short white lobes scarcely exerted from its reddish lobed cup; capsule sessile, 6-10 mm. long ca. 2 mm. thick, somewhat fusiform in outline, narrowed at base, 4-nerved, obtusely 4-angled above; seeds 1-2, brown.

## KEY TO VARIETIES

Ovary and capsule glabrous

Hypanthium minutely puberulent.....2a. *G. parviflora* var. *typica*

Hypanthium glabrous.....2b. forma *glabra*

Ovary and capsule short-pubescent.....2c. var. *lachnocarpa*

2a. *G. parviflora* Dougl. var. *typica* n.nom.

*G. parviflora* Dougl. ex Hook., Fl. Bor. Am. 1: 208. 1834. *Schizocarya micrantha* Spach, Ann. Sci. Nat. II, 4: 283. 1835. *Gaura micrantha* D. Dietr., Syn. Pl. 2: 1297. 1840. *G. mollis* Nutt. ex Torr., Ann. Lyc. N. Y. 2: 200. 1828, not HBK. in 1823.

Hypanthium puberulent, 2-3 mm. long; sepals 2-3 mm. long, mostly glabrous, sometimes puberulent; ovary and capsule glabrous.

Type locality, "Sandy banks of the Wallawallah River, North-west coast of America." Grows best as a ruderal and is common in waste and disturbed places over a large area from eastern Washington to the Mississippi Valley and northern Mexico. Sometimes introduced farther east: MASS.: Cambridge, *Morong in 1886* (NY); INDIANA: Michigan City, *Mell 111* (US); ILLINOIS: Romeo, *Umbach in 1897* (US). Other representative material, Rocky Mts., *Nuttall* (K, NY). MISSOURI: Joplin, *Palmer 2591* (G, NY, US). SO. DAK.: Deadwood, *Murdoch 4331* (G, NY). NEBRASKA: Minden, *Hapeman in 1928* (P); St. James, *Clements 2632* (G, NY). KANSAS: Manhattan, *Norton in 1892* (NY); Osborn City, *Shear 145* (G, P, US). OKLAHOMA: Bridgeport, *Munz 13577* (P); Calvin, *Munz 13574* (P). COLORADO: Denver, *Jones 656* (NY, P); Naturita, *Payson 118* (G). WYOMING: Gardiner River, Yellowstone Nat. Park, *A. & E. Nelson 5986* (G, NY, US); Two Bar Ranch, Blue Grass, *Nelson 376* (G, NY, US). IDAHO: King Hill, Elmore Co., *Nelson & Macbride 1096* (G, NY, P, US); Falk's Store, Canyon Co., *Macbride 329* (G, NY, US). WASHINGTON: low banks of Walla Walla River, *Douglas*,



Herb. Hookerianum (K, photo at P); Wawawai, Whitman Co., *Elmer* 898 (NY, P, US). OREGON: Snake River bottom, Union Co., *Cusick* 939 (G); The Dalles, *Peck* 9916 (P). NEVADA: Battle Mt. *Hitchcock* 613 (US). UTAH: Springdale, *Jones* 5256 (NY, P, US); Parley's Canyon, Wasatch Mts., *Stokes in 1900* (NY, US). ARIZONA: Navaho Reservation, *Vorkies* 120 (G, NY); Chiricahua Mts., *Blumer* 1776 (G, NY, US). NEW MEXICO: Farmington, San Juan Co., *Standley* 6924 (US); Albuquerque, *Jones in 1884* (P). TEXAS: Jeff Davis, *Cory* 2138 (P). S. Felipe de Austin, *Drummond* 46, type coll. of *Schizocarya micrantha* (Del, G, NY); Del Rio, *Jones* 25877 (P). CHIHUAHUA: Chihuahua, *Palmer* 190, in part (G, NY, US), SONORA: Cochuto, *Hartman* 96 (G, NY, US).

Intergrading freely with both of the following:

2b. *G. parviflora* var. *typica* forma *glabra* new form.

Hypanthium glabrous, 2–3 mm. long; sepals glabrous, 2–3 mm. long; ovary and capsule glabrous. (Hipanthium glabrum, 2–3 mm. longum; sepalis glabris, 2–3 mm. longis; ovario capsulaque glabris).

Type, Deer Run, west central Colorado, *Baker* 94, June 11, 1901, at 4700 ft., Pomona College Herbarium No. 32745; isotypes at Gray, New York, U. S. Ranging more or less widely with var. *typica*. Representative material, MISSOURI: St. Louis, *Sherff* 405 (G); Joplin, *Palmer* 2494 (G). OKLAHOMA: Hollis, Harmon Co., *Stevens* 1100 (G, NY). TEXAS: Weatherford, *Tracy* 7822 (G, NY, US); San Antonio, *Clemens* 695 (NY, P). LOUISIANA: Mississippi banks, *Langlois* 96 (NY). NEBRASKA: Calahan, *Williams in 1889* (US). KANSAS: Wichita, *Smyth* 236 (US). COLO.: Durango, *Baker, Earle & Tracy* 493 (G, NY, P, US). NEW MEXICO: Ft. Bayard Watershed, Grant Co., *Blumer* 72 (G, NY); Kingston, Sierra Co., *Metcalfe* 1241 (G, NY, P, US). ARIZONA: Ramsay Canyon, Huachuca Mts., *Jones* 24941 (P). Some collections show complete intergradation of this rather trivial form with var. *typica*, for example *Metcalfe* 159, Mangas Springs, N. M. (G, NY, P, US) and *Earle* 230 from Lincoln, N. M. (NY).

2c. *G. PARVIFLORA* Dougl. var. *LACHNOCARPA* Weatherby, *Rhodora* 27: 14, 1925.

*G. australis* Grisebach, Goett. Abh. 24: 132. 1879.

Hypanthium 1.5–2.5 mm. long, with short mostly divergent pubescence; sepals 1.5–2 mm. long, strigulose or with divergent puberulence; capsule with divergent pubescence.

Type locality, Austin, Texas. With a more southern range than that of var. *typica*, although with some overlapping, it occurs from Missouri and

Utah to Mexico, also in Argentine. Representative material, MISSOURI: Courtney, *Bush* 7738 (G, NY). ALABAMA: Montgomery, *Harper* in 1924 (G, NY, US), very possibly an introduction. TEXAS: Austin, *Young* 95, type (G), *E. Hall* 216 (G, NY, P, US); Kerrville, *Heller* 1768 (G, NY, US); Belmont, Gonzales Co., *Munz* 13338 (P). NEW MEXICO: Mesilla, *Crozier* in 1897 (G). ARIZONA: Casa Grande, *Loomis* 1160 (P); Colorado Valley near Ft. Mojave, *Cooper* in 1860-'61 (G, US). UTAH: Salt Lake City, *Jones* 1460 (NY, P, US); St. George, *Craig* 1398 (P). BAJA CALIFORNIA: San José del Cabo, *Anthony* 330 (G, P, US); Todos Santos, *Jones* 24137 (P); Muleje, *E. Palmer* 11, in 1887 (G, US). SONORA: Hermosillo, *Rose, Standley & Russell* 12465 (NY, US); Alamos, *Rose, Standley & Russell* 12961 (NY, US). CHIHUAHUA: Lake Santa Maria, *Nelson* 6406 (US). COAHUILA: Saltillo, *E. Palmer* 213, in 1898 (G, NY, US). DURANGO: Durango, *E. Palmer* 102, in 1896 (G, NY, US). SINALOA: Culliacan, *Rose, Standley & Russell* 14867 (NY, US). ARGENTINE: Sierra de Córdoba, Capilla del Desierta, *Barros* in 1925 (G); Sierra Chica, Córdoba, *Lossen* 226 (G); Sierra Grande, Córdoba, *Burkart* 7328 (P); between Mina Argentia u Yerbabuena in foothills of Cerro de Oroosu, Córdoba, *Hieronimus* in 1876, no. 399, ex Herb. Goettingen (P, Ber).

This variety intergrades freely with var. *typica*, as is evidenced by *Clark* 314 from Boise, Idaho (US); *Eastwood* 31 from Denver, Colo. (US); *Bates* from Long Pine, Nebr. (G). In these collections there is some pubescence on the fruits, but not enough to be representative of var. *lachnocarpa*. Material from Baja California tends to have smaller flowers and a more glabrous style than do other plants, but the tendencies do not seem to be definite enough to merit recognition. South American material matches very well that from North America, especially the small-flowered strain from Baja California. Varietal rank for this pubescent-fruited concept as opposed to the smooth-fruited sort which I am recognizing only as a form, seems justifiable because of the tendency to small flowers and the more distinctly southern range.

3. GAURA BIENNIS L., Sp. Pl., 347. 1753.

Biennial or winter annual, 3-30 dm. high, from a somewhat fusiform fleshy root; stem erect, pubescent to villous, simple below, openly much branched above; leaves soft-pubescent to glabrate, well distributed; rosette leaves oblanceolate, 1-3 dm. long, 2-4.5 cm. wide, subentire to irregularly sinuate-dentate, narrowed into short winged petioles; cauline leaves numerous, oblong-lanceolate to lance-ovate, acute or acuminate at both ends, remotely denticulate, 3-10 cm. long, 1-2.5 cm. wide, narrowed gradually into very

short winged petioles, often with short axillary fascicles; floral bracts 1-4 mm. long, deciduous, ovate, acute; flowers open in evening, spicate, the slender spikes in open terminal panicles 1-5 dm. long; hypanthium slender, usually reddish, 5-7 mm. long, short-pubescent without, with dense curly pubescence within; sepals generally red, pubescent, 6-8 mm. long, narrow, reflexed in pairs at anthesis, without free tips in bud; petals white, aging pink, clawed, spatulate-elliptic, about 5 mm. long, the two upper ascending, the 2 lower horizontal; stamens subequal, the filaments flattened, glabrous, 5-7 mm. long, with very minute basal ovate, somewhat flattened scale, whitish; anthers white to pink, 2.5-3 mm. long, linear; style somewhat longer than stamens, reddish, with curly pubescence at very base; stigma-lobes ca. 1 mm. long; capsule pubescent, sessile, ovoid-fusiform, 4-angled, broadly 4-ribbed, acute at both ends, 4-7 mm. long, 1-few-seeded.

## KEY TO VARIETIES

- Stems villous, as well as short-pubescent; inflorescence with short gland-tipped hairs as well as non-glandular ones; leaves green, glabrate. .... 3a. var. *typica*.  
 Stems short-pubescent only; inflorescence with numerous short non-glandular hairs only; leaves somewhat canescent. .... 3b. var. *Pitcheri*

3a. *Gaura biennis* L. var. *typica* n.nom.

*G. biennis* Ll., Sp. P., 347. 1753; Curtis, Bot. Mag., pl. 389. 1797.

Stems, spreading-villous as well as short-pubescent; leaves glabrate, at least not canescent; hypanthium, buds, etc., with some short spreading gland-tipped hairs as well as some non-glandular ones.

Type locality, "Habitat in Virginia, Pennsylvania" according to Linnaeus. He refers to Plukenet (Alm., pl. 202, f. 7); this figure and the plant specimen in the Sloane Herbarium at British Museum from which the drawing seems to have been made, are apparently *Oenothera parviflora* L. In the Linnaean Herbarium are two specimens labeled *Gaura biennis*; both of which fit our concept.

The variety ranges from southern New England to Virginia and Missouri and Iowa. Representative material, MASSACHUSETTS: Cambridge, *Morong in 1886* (NY). CONNECTICUT: New Haven, *Eaton* (G, P); Bristol, *Bishop in 1897* (G, US). ONTARIO: Ft. Erie, *Kolles in 1925* (NY). NEW YORK: Ithaca, *Munz 767* (P), *Coville in 1884* (US); Watkins, *House 20109* (NY, US). NEW JERSEY: Princeton, *Peters in 1885* (NY). DELAWARE: Hollyoak, *Commons in 1896* (NY). PENNSYLVANIA: Liverpool, Perry Co., *Munz 13408* (P); Northampton *Churchill in 1923* (G, P). MARYLAND: Kensington, Montgomery Co., *Munz 13474* (P). WEST VIRGINIA: Mt. Crawford, Rockingham Co., *Heller & Halbach 1200* (G, NY, US); White Sulphur Springs, *Munz 13492* (P). VIRGINIA: Bedford Co., *Curtiss in 1871* (G, NY). NORTH

CAROLINA: Cherokee, Swain Co., *Munz* 13522 (P); Biltmore, *Biltmore Herbarium No. 458a* (G, NY, US). TENNESSEE: La Follette, Campbell Co., *Munz* 13586 (P); Elizabethton, *Wiegand & Manning* 2162 (G). KENTUCKY: Wilmore, Jessamine Co., *Anderson* 585 (G). OHIO: Mansfield, *Wilkinson* 3425 (G, P); Toledo, *Young in 1884* (G, NY). INDIANA: Near Ft. Wayne, *Deam* 21688 (NY). ILLINOIS: Peoria, *McDonald in 1904* (G); Urbana, *Pease* 13041 (G). IOWA: Vinton, *Davis* 6 (US). MISSOURI: Gregory Landing, Clark Co., *Drouet* 1700 (P); Springfield, *Standley* 8348 (US).

3b. *G. BIENNIS* var. *PITCHERI* Pickering ex Torr. & Gray, Fl. No. Am. 1: 517. 1840.

*G. Pitcheri* Pickering, 1. c, in synonymy; *G. Pitcheri* (Pickering) Small, Fl. S. E. U. S., 847, 1335. 1903.

Stems and leaves canescent, strigulose; hypanthium, buds, inflorescence strigulose or puberulent, not glandular.

Type locality, Red River. Ranging from Illinois to Nebraska and Texas. Representative material, ILLINOIS: Elk Grove, Cooke Co., *Buhl* F736 (P); St. Clair Co. *Eggert in 1877* (G). IOWA: Dubuque, *Mertz in 1877* (NY); Redfield, Dalles Co., *Allen in 1867* (G). NEBRASKA: Lincoln, *Webber in 1887* (US); Omaha, *Cleburne* (P). KANSAS: Riley Co., *Norton* 169 (G, NY, US); Lawrence, *Snow* (US). MISSOURI: St. Louis, *Drummond in 1832* (NY); Monett, Barry Co., *Munz* 13556 (P); Van Buren, Carter Co., *Munz* 13589 (P). ARKANSAS: Little Rock, *Hasse in 1885* (NY). OKLAHOMA: Tulsa, *Stevens* 2992 (G); Pawhuska, Osage Co., *Stevens* 1932 (G, NY, US). TEXAS: Decatur to Alvord, Wise Co., *Ferris & Duncan* 3324 (NY). Without definite locality, Red River Dr. *Pitcher*, type (NY).

Intergrades freely with var. *typica*, as evidenced by many specimens, for example: Carthage, Jasper Co., Mo., *Eggleston* 12072 (NY); Grinnell, Ia., *Jones* (P); Carroll, Ia., *Pammel* 23 (G, NY, US), all of which have the stem-pubescent of *Pitcheri* and bud-pubescent of *typica*. Examples with stem of *typica* and buds of *Pitcheri* are: Mira, Ill., *Gleason* 1980 (G); Peoria, *McDonald in 1889* (G); and Utica, Ill., *Clemens in 1909* (P).

4. *GAURA NEOMEXICANA* Wooton, Bull. Torrey Club 25: 307. 1898.

Biennial or perennial herb, from thick root; stems one to several from the base, erect, simple or few-branched above, 5-8 dm. high, greenish or reddish, pubescent; basal leaves 8-15 cm. long, the blades oblanceolate, subentire or sinuate-denticulate, pubescent, 4-7 cm. long, 1-2 cm. wide, narrowed into almost equally long winged petioles; cauline leaves mostly lanceolate, 5-10 cm.

long, 8–16 mm. wide, strigose, acute, subentire to minutely sinuate-denticulate, gradually narrowed into short winged petioles; upper ones reduced, subsessile; floral bracts lanceolate, pubescent, acuminate, 5–8 mm. long, caducous; inflorescence spicate, simple or few-branched, 1–4 dm. long in fruit; hypanthium slender, 8–12 mm. long pubescent, without, with a white matted curly pubescence within; sepals more or less red, reflexed separately in anthesis, linear-lanceolate, 9–11 mm. long; petals pink, short-clawed, spatulate to narrowly obovate, 8–10 mm. long; stamens subequal, filaments slightly enlarged upward, about as long as petals; with minute thickened basal scale; anthers linear, 3–4 mm. long; style somewhat longer than stamens, pubescent at very base; stigma-lobes surpassing the indusium 1–1.5 mm.; capsule 7–10 mm. long, fusiform, obtusely 4-angled and with a median nerve on each face, apparently 1-seeded.

*G. neomexicana* is undoubtedly very closely related to *G. biennis* and differs by being less branched, lower, more perennial, with larger fruits and flowers and a more western range. I am recognizing two varieties which differ from each other in much the same way as do those of *G. biennis*.

#### KEY TO VARIETIES

Stem spreading-villous as well as short-pubescent; inflorescence with some gland-tipped hairs as well as non-glandular ones. So. Colo. and New Mex. .... 4a. *G. neomexicana* var. *typica*  
Stem appressed- and short-pubescent only; inflorescence with non-glandular hairs only. No. Colo. .... 4b. *G. neomexicana* var. *coloradensis*

#### 4a. *G. neomexicana* Woot., var. *typica* n.nom.

*G. neomexicana* Woot., Bull. Torrey Club 25: 307. 1898.

Hair on stem of two kinds: long spreading and short appressed; inflorescence with gland-tipped and non-glandular hairs.

Type locality, White Mts., Lincoln Co., New Mex. Material seen, COLORADO: Piedra Paradra, *Newberry* in McComb Exped., 1859 (US); Piedra Creek, *Wooton* 2738 (US); Piedra, La Plata Co., *Baker* 491 (NY, P, US); Pagosa Springs, Archuleta Co., *Baker* 490 (G, NY, P, US). NEW MEXICO: Chama, Rio Arriba Co., *Standley* 6783 (NY, US); White Mts., Lincoln Co., *Wooton* 204, type coll., (NY, US); Cloudcroft, Otero Co., *Wooton* in 1899 (G, NY, P, US); Tularosa Creek, 3 mi. south of Mes-calero Agency, Otero Co., *Wolf* 2768 (G, P); James Canyon, Sacramento Mts., Otero Co., *Wooton* in 1899 (US).

#### 4b. *G. neomexicana* Woot. var. *coloradensis* (Rydb.) n.comb.

*G. coloradensis* Rydb., Bull. Torrey Club 31: 572. 1904.

Hair of stem short and appressed, of inflorescence not at all glandular.

Type locality, Ft. Collins, Colo. Material seen, COLORADO: Ft. Collins, *Cowen*, July 8, 1895, type coll. (G, NY), *Cowen* July 1, 1895 (US), meadows east of college, *Crandall* 1308 (NY).



5. *GAURA MACROCARPA* Rothrock, Proc. Amer. Acad. 6: 353. 1864-65.

Apparently perennial from rather woody caudex, with several ascending herbaceous stems, these simple or branched, 2-6 dm. tall, more or less scabrous-hirtellous throughout, cinereous; basal leaves oblanceolate to oblong-lanceolate, 2-5 cm. long, sinuate-denticulate, more or less wavy, scabrous-hirtellous, hispid-ciliate, short-petioled; cauline leaves rapidly reduced up the stem, lower ones lanceolate, with 1 or 2 teeth on each side, 1-2 cm. long, 4-6 mm. wide; upper ones linear-oblong, subentire, 5-15 mm. long, 1-2 mm. wide, all hispid-ciliate, subcinereous; floral bracts lanceolate to subulate, rather persistent, 3-5 mm. long; spikes few-flowered, 5-12 cm. long, scarcely, peduncled, nodding at tip, scabrous-hirtellous; hypanthium strigulose without, slender, 8-10 mm. long, short-pubescent within; sepals lance-linear, 6-7 mm. long, strigulose, reflexed separately; petals white, turning red in age, rhombic-ovate, 5 mm. long and wide; stamens subequal; filaments strongly flattened, 3-4 mm. long; anthers 4-5 mm. long; style slightly surpassing stamens, short-puberulent at base; stigma-lobes ca. 1 mm. long; capsule canescent-puberulent, narrowly fusiform, straight or curved, slightly thicker in upper half, 10-15 mm. long, 1.5-2 mm. thick, terete, ribbed but not angled, sometimes somewhat narrowed at base into a short terete portion up to 3 mm. long.

Type locality, "valley of the Limpio," west Texas. Material seen, TEXAS: White Rose Pass, Davis Mts., *Cory*, May 4, 1936 (P); Ft. Davis, *Jones* 25880 (P); Davis Mts., *Tracy & Earle* 127 (NY, US); Ft. Davis, *Palmer* 34558 (NY, US), *Young* 1681 (US); valley of the Limpio, *Wright* 1079, type coll. printed "1879" by Rothrock (G, US); Limpio Mts., *Harvard* 125 (G, US); Jeff Davis Co., *Cory* 2137 (P); San Felipe Springs, Val Verde Co., *Cory* 8998 (P); Boquillas, Brewster Co., *Cory* 2139 (P); 17 miles south of Alpine, *Cory* 9278 (P). COAHUILA: San Lázaro, Castaños, *Wynd & Mueller* 145 (US) CHIHUAHUA: Chihuahua, *Pringle* 1497 in part (G), *Palmer* 195, in 1908 (NY, US).

As I understand this species, it is quite near to *G. odorata*, but differs in being scabrous, having shorter leaves and narrow fruit.

6. *GAURA LINDHEIMERI* Engelm. & Gray, Boston Journal Nat. Hist. 5: 217. 1845.

Perennial, simple or branched at base, the stems erect, 5-9 dm. tall, strigose and sometimes also short-hirsute, usually freely branched above; lower cauline leaves spathulate to oblong-ob lanceolate, mostly sinuate-dentate, or -denticulate, acute to obtuse, 3-9 cm. long, 7-15 mm. wide, subsessile or with short winged petiole, strigose; upper ones reduced, subentire; floral bracts ovate to lanceolate, 5-10 mm. long, thin, caducous, more or less villous; spikes simple, or usually branched and in open panicles 2-6 dm. long, on

peduncles 5 or more cm. long; axes glabrous or usually more or less pilose and also glandular-pubescent, nodding at tips; hypanthium usually reddish, slender, 5–8 mm. long, externally with scattered gland-tipped hairs and usually some longer non-glandular ones, internally with white interwoven hairs; sepals more or less reddish, pilose and glandular-pubescent, 12–15 mm. long, lance-linear, separately reflexed in anthesis; petals white, changing to rose, spatulate-rhomboid, short-clawed, 12–20 mm. long; stamens subequal, the filaments slightly flattened upward, 10–15 mm. long; anthers red, ca. 4 mm. long; style slightly exceeding stamens, pubescent at base; stigma-lobes ca. 0.5 mm. long; fruit elliptic-oblong, about equally narrowed at both ends, 7–9 mm. long, sharply 4-angled, each face 2 mm. wide, 1-ribbed and somewhat furrowed apically, subglabrous to scattered-pilose.

Type locality, apparently Houston, Texas. Growing in prairie sod, southeastern Texas and adjacent Louisiana and Mexico. Representative material, TEXAS: Houston, *Rose* 18127 (NY, US), *Palmer* 12792 (G, NY, US), *Munz* 13339 (P); Sheldon, *Reverchon* 3842 (G, P, US); 3 miles east of Liberty, Liberty Co., *Munz* 13342 (P); 2.6 mi. east of Camp Jackson, Hardin Co., *Cory* 19765 (P); Amelia, Jefferson Co., *Cory* 11091 (P); Beaumont, *Reverchon* 3841 (G, P, US). LOUISIANA: Jennings, Jefferson Davis Parish, *Munz* 13340 (P), *Palmer* 7612 (NY, US); Mermentau, Acadia Parish, *Degner* 5120 (NY); Centreville, St. Mary Parish, *Munz* 1588 (P). MISSISSIPPI: Grant Batture Id., *Howell* 746 (US). COAHUILA: Saltillo, *Nil in* 1910 (G, NY). NUEVO LEON: Monterrey, *Arsène in* 1911 (NY).

This species is characterized by its large flowers, pilose sepals and elliptic fruit. It is rather variable in pubescence, such collections as *Reverchon* 3841, *Palmer* 7612, and *Munz* 13340 being partly or quite hirsute.

7. *GAURA ANGUSTIFOLIA* Michx., Fl. Bor. Am. 1: 226. 1803.

Winter annual, or biennial?, 6–18 dm. tall, mostly erect, simple below, with open divaricate slender branches above; rosette-leaves narrowly oblanceolate, 5–18 cm. long, 7–15 mm. wide, irregularly sinuate-dentate to almost runcinate, acute, narrowed gradually into a winged petiole which varies from 1–7 cm. in length; main cauline leaves narrowly oblanceolate to narrowly lanceolate, subsessile or short-petioled, 3–6 cm. long, 5–8 mm. wide, subentire to sinuate-denticulate, acute; upper cauline leaves gradually reduced, lance-linear, 1–3 cm. long, 1–3 mm. wide, subentire; floral bracts lance-linear, 2–4 mm. long, caducous; spikes 1–3 dm. long, very slender, simple or openly branched; hypanthium slender, more or less reddish, 3–5 mm. long, pubescent within with rather long curly hairs; sepals somewhat reddish, 5–7 mm. long, separately reflexed or more or less adherent in anthesis; petals white or pink, spatulate to spatulate-oblong, 4–6 mm. long; stamens slightly unequal, 4–5



mm. long; filaments somewhat flattened, glabrous, each with very minute fleshy basal scale; anthers oblong, ca. 1 mm. long, white to pinkish; style slightly exceeding stamens, pubescent in lower part; stigma-lobes ca. 0.5 mm. long; capsule elliptic to narrowly ovoid, rather sharply 3-4-angled, 5-10 mm. long, narrowed into pedicel-like base 0.5-1.0 mm. long, apparently 1-2-seeded.

Exceedingly variable as to pubescence and length of capsule, of which the wings may be 3 or 4, both forms often occurring on the same plant. The following varieties are not very clear, but having some definiteness in range as well as pubescence seem worth recognition.

#### KEY TO VARIETIES OF *G. ANGUSTIFOLIA*

- |  |                          |
|--|--------------------------|
| Capsules pubescent; sepals pubescent. No. Car. to Fla. and Ala.    | 7a. var. <i>typica</i>   |
| Pubescence of sepals and capsules loose and spreading.             | 7b. var. <i>strigosa</i> |
| Pubescence of sepals and capsules fine and closely appressed. Fla. |                          |
| Capsules and sepals glabrous.                                      | 7c. var. <i>simulans</i> |
| Stem, leaves and axes of inflorescence pubescent. So. Fla.         | 7d. var. <i>Eatonii</i>  |
| Stem, leaves and inflorescence-axes glabrous. Punta Rassa, Fla.    |                          |

#### 7a. *G. angustifolia* Michx. var. *typica* n.nom.

*G. angustifolia* Michx., Fl. Bor. Am. 1: 226. 1803. *G. undulata* Desf., Tableau de l'Ecole de Bot., ed. 2, 196. 1815, nomen. *G. fruticosa* Jacq., Coll. 1: 142, pl. 181. 1786 and Ic. Rar. 3: pl. 457. 1786-1793; not *G. fruticosa* Loeffl., Iter Hispan., 248. 1758. *G. longiflora* Spach, Nouv. Annal. Mus. Paris 4: 380. 1835.

Stem strigose; leaves somewhat strigose, especially on the veins of under surface and on margins; inflorescence pubescent throughout short puberulent only (or with some longer additional hairs); capsule likewise pubescent, even short-villous.

Type locality, "in Carolina inferiore." Ranging from No. Car. to Fla. and Ala. Representative material, WITHOUT LOCALITY: *G. fruticosa*, en h.v. paris 1787, Herb. Jussieu (Paris); Hort. Paris 1790 (BM, photo at G & P); "*G. angustifolia*," Herb. Michx. (Paris). NORTH CAROLINA: Vandemer, Pamlico Co., *L. F. & F. R. Randolph* 856 (G); Wilmington, *Coville* 149 (US). SOUTH CAROLINA: Beaufort, *Lewis* 192 (NY); Pine Island, *Harris C* 19734 (US); 14 mi. east of Waterboro, *Wiegand & Manning* 2160 (G). GEORGIA: Wilmington Island, *Hopkins* 24 (NY). ALABAMA: Rosemary, Hale Co., *Harper* 3253 (NY, US); Cedarpoint, *Mohr in* 1893 (US); Mobile, *Mohr in* 1895 (US). FLORIDA: near Jacksonville, *Drummond in* 1833, apparently type coll. of *longiflora* (G, K, photo at P), *Curtiss* 895 (G. NY, US); Lake City, *Wiegand & Manning* 2161 (G); Ft. Pierce, Santa Lucie Co., *Burgess* 735 (NY); Cape Canaveral, Broward Co., *Burgess* 654 (NY).

7b. *G. angustifolia* Michx. var. *strigosa* n.var.

Stem, leaves and inflorescence (hypanthium sepals, ovaries) finely strigulose.

Type, Eustis, Lake Co., Fla., *G. V. Nash 1464*, July 16–31, 1894 (NY); isotypes at Gray and U. S. National Herbarium. Found in northcentral Florida. Material seen, FLORIDA: St. Charles, *Rugel in 1843* (NY); Eustis, Lake Co., *Hitchcock in 1894* (P); St. Petersburg, *Beckwith 728* (US); So. Jacksonville, *Lighthipe 277* (NY), *276* (NY); Appalachicola, Gulf Co., *Chapman* (NY, US); Duval Co., *Fredholm 234* (P), *5240* (US); Alligator Harbor, *Tracy 7599* (US); Tallahassee, *Berg* (NY); Tampa, *Garber in 1876* (US); St. Vincent Island, *McAtee 1750* (US).

7c. *G. angustifolia* Michx. var. *simulans* (Small) n.comb.

*G. simulans* Small, Bull. N. Y. Bot. Garden **3**: 432. 1905.

Stems pubescent; leaves pubescent; inflorescence axes pubescent; hypanthium, sepals and ovaries glabrous.

Type locality, between Cocoanut Grove and Cutler, Dade Co., Fla. Range in southern Florida. Material seen, FLORIDA: Myers, Lee Co., *Hitchcock 123* (G, NY, US); 8 miles southeast of Ft. Myers, *Standley 474* (G, P); Buckingham, Lee Co., *Moldenke 1008* (NY, US); Miami, *Garber in 1877* (G, US in part), *Small & Small 4822* (NY), *Small, Carter & Small 3255* (NY); Silver Palm School, Dade Co., *Small 2195* (NY); between Cocoanut Grove & Cutler, *Small & Wilson 591* (NY), *Small & Carter 766*, type coll. (G, NY); Miami Beach, *Moldenke 584* (NY, US); between Miami & Kendall Station, *Small & Carter 2606* (NY); Virginia Key, *Britton 102* (NY); Sykes Hammock, Dade Co., *Small et al. 5765* (NY).

7d. *G. angustifolia* Michx. var. *Eatonii* (Small) n.comb.

*G. Eatonii* Small, Fl. S.E. U.S., ed. 2, 1353, 1375. 1913.

Stems, leaves, inflorescence and fruit glabrous.

Type locality, Punta Rassa, Lee Co., Florida. Material seen, Punta Rassa, *Eaton 1107* (G), *1289*, type (NY), *Standley 261* (G, NY, US), *12673* (US) Shell Island, *Tracy 7598* (G, NY, US); Naples, *Degner 4943* (NY); Salvista, *Moldenke 1032a* (NY); Ft. Myers, *Moldenke 917* (NY), *789* (NY); Captiva, Lee Co., *Orron in 1915* (US); Clearwater Beach, *Beckwith in 1921* (US).

8. *GAURA FILIFORMIS* Small, Bull. Torrey Club **25**: 617. 1898.

Biennial, erect, 6–25 dm. tall, more or less canescent-strigose throughout, simple at base, freely and divaricately branched above, the ultimate branchlets almost filiform; rosette-leaves not seen; lower cauline leaves lanceolate, 4–10 cm. long, 8–15 mm. wide, subentire to sinuate-dentate, acute, narrowed gradually into very short winged petioles; upper leaves reduced, lance-linear, acuminate, subsessile, quite entire, 1–3 cm. long, 2–4 mm. wide; floral bracts

almost linear, 4-6 mm. long, caducous; inflorescence of slender spikes in an open panicle, 1-3 dm. long, finely canescent-strigose throughout; hypanthium slender, 4-6 mm. long, strigulose without, with heavy white pubescence within; sepals narrow, 8-10 mm. long, usually more or less adherent in anthesis; petals "pink-purple," about 7 mm. long, clawed, spatulate; stamens somewhat unequal, with flattened filaments 6-7 mm. long; anthers linear, 2.5-3 mm. long, purplish; style pubescent at base, exceeding the stamens by 2-4 mm.; stigma-lobes 0.4-0.8 mm. long; capsule quite sessile, canescent, 3-6 mm. long, somewhat fusiform, 4-angled, each side with a median rib; seeds 1-2.

## KEY TO VARIETIES

Hypanthium and sepals strigulose.....8a. *G. filiformis* var. *typica*  
Hypanthium and sepals with spreading hairs.

Hairs of hypanthium and sepals less than 0.5 mm. long, some of them gland-tipped.....

.....8b. var. *Kearneyi*

Hairs of hypanthium and sepals about 1 mm. long, not gland-tipped.....8c. var. *Munzii*

8a. *Gaura filiformis* Small var. *typica* n.nom.

*G. filiformis* Small, Bull. Torrey Club 25: 617. 1898. *G. exaltata* Engelm. & Gray, Boston Journ. Nat. Hist. 5: 44. 1845, nomen nudum.

Hypanthium and sepals with appressed non-glandular hairs.

Type locality, Texarkana, Miller Co., Ark. Range, from Miss. and La. to Ark. and eastern Texas. Representative material, MISSISSIPPI: Biloxi, *Tracy 5071*, in part (G); Ocean Springs, *Pollard 1021* (G, NY, US); Agricultural College, Oktibbeha Co., *Pollard 1320* (G, NY, US); Shelton, *Rhoades in 1931* (G). LOUISIANA: Opelousas, without collector (US); Alexandria, *Hale* (NY); Feliciana & Opelousas, *Carpenter* (NY). ARKANSAS: Texarkana, A. A. & E. G. *Heller 4138*, type coll. (G, NY, US); 6 mi. north of Hot Springs, *Scully 377* (P); Ft. Smith, *Bigelow in 1853-4* (US). TEXAS: Richmond, Ft. Bend Co., *Palmer 6655* (P, US); Houston, *Lindheimer 239* number referred to under *exaltata* (G, US); Dallas, *Reverchon 39* (G); Morgan's Point, Harris Co., *Cory 8140* (P); 7 miles west of Dickinson, Galveston Co., *Cory 11398* (P).

This variety is often easily confused with *G. biennis* var. *Pitcheri*, but in a mature enough condition, the more sharply angled fruits of *filiformis* are distinctive.

8b. *G. filiformis* Small var. *Kearneyi* n.var.

Hypanthium and sepals with some very short spreading hairs, some of which may be gland-tipped. (Hipantium et sepala cum capillis curtis divaricatisque, cum alteris glandulosis.)

Type, from along railroad track, Starkville, Miss., Sept. 28, 1896 *T. H. Kearney Jr.*, (NY). Other material seen, ALABAMA: Cocoa, Choctaw Co., *Schuchert in 1896* (NY, US). MISSISSIPPI: Biloxi, *Tracy 5071*, (NY in part, US), *Lloyd & Tracy 224* (NY); Ocean Springs, *Seymour 84* (G).

TEXAS: seven miles west of Lufkin, Angelina Co., *Cory* 10633 (P); Roston, Lamar Co., *Cothran* 17479 (P); Newton, Newton Co., *Cory* 10906 (P).

8c. *G. FILIFORMIS* Small var. *MUNZII* Cory.

Hairs of hypanthium and sepals non-glandular, spreading, ca. 1 mm. long.

Type locality,  $6\frac{1}{2}$  miles north of High Island, Chambers Co., Texas. Specimens seen,  $6\frac{1}{2}$  miles no. of High Island, Texas, *Cory* 20179 (P), 20180 (P);  $6\frac{1}{2}$  miles west of Alvin, Brazoria Co., *Cory* 11399 (P).

9. *GAURA SUFFULTA* Englm. ex Gray, Boston Journ. Nat. Hist. 6: 190. 1850.

Apparently winter annual or biennial, 2-8 dm. tall, usually few-branched at base or above, and ascending, sometimes simple and erect; stems spreading-villous in leafy portion; basal leaves in a rosette, oblanceolate, 5-18 cm. long 1-2.5 cm. wide, runcinate-pinnatifid, usually subglabrous except for the villous margins, veins and petioles; petioles winged, making up  $\frac{1}{4}$ - $\frac{1}{2}$  length of whole leaf; cauline leaves rather crowded, oblanceolate to lanceolate, 4-10 cm. long, 1-2 cm. wide, acute, sinuate to subentire, short-villous on veins and margins, with winged petioles 4-15 mm. long; uppermost lance-linear, 1-3 cm. long; floral bracts glabrous, oblong-ovate, 6-10 mm. long, acuminate, reddish-veined, caducous; spikes glabrous, simple, becoming 1-3.5 dm. long, and on a naked, more or less villous peduncle 5-15 cm. long; hypanthium slender, somewhat reddish, 5-12 mm. long, with dense white pubescence within; sepals oblong-linear, with some red veining, 8-10 mm. long, reflexed singly or in pairs at anthesis; petals white, aging pink, oblong to oblong-spatulate, 9-10 mm. long; stamens subequal filaments slightly flattened, 5-6 mm. long, with basal scale; anthers linear-oblong, 4-5 mm. long, somewhat reddish; style pubescent at base, somewhat exceeding stamens; stigma-lobes whitish, ca. 0.6 mm. long; capsule sessile, ovoid, 4-7 mm. long, glabrous, wing-angled above, obtusely angled below, with median rib on each face; seeds 1-few.

KEY TO VARIETIES

- Hypanthium glabrous, 5-7 mm. long; sepals glabrous except sometimes for ciliate margins..... 9a. *G. suffulta* var. *typica*  
 Hypanthium glandular-puberulent, 10-12 mm. long; sepals glandular-puberulent..... 9b. var. *terrellensis*

9a. *Gaura suffulta* Engelm. var. *typica* n.nom.

*G. suffulta* Engelm. ex Gray, Boston Journ. Nat. Hist. 6: 190. 1850.

Hypanthium and sepals mostly glabrous except for some hair along the edges of the latter; hypanthium 5-7 mm. long.

Type locality, New Braunfels, Texas. Ranging widely in Texas, rare in Okla. and Tamaulipas. Representative material, OKLAHOMA: Arbuckle Mts., Murray Co., *Goodman* 2448 (P). TEXAS: Austin, *Hall* 212 (G, NY, P, US); New Braunfels, *Lindheimer* 611, type coll. (G, NY, US); Dallas, *Curtiss dist.* 896 (G, NY, US); San Antonio, *Clemens* 697 (NY, P); Midland, Midland Co., *Cory* 8743 (P); Ozona, Crockett Co., *Jones* 25878 (P); Five-mile Creek, Upton Co., *Cory* 583 (P); Ranch Experiment Sta-

tion, Edwards Co., *Cory* 15268 (P). TAMAULIPAS: Matamoros, *Berlandier* 2313=883 (K, photo at P). As an escape at Philadelphia, Pa., *Martindale* in 1882 (US).

9b. *G. suffulta* Engelm. var. *terrellensis* n.var.

Hypanthium and sepals glandular-pubescent; hypanthium 10-12 mm. long. (Hipanthium et sepala glanduloso-puberulenta; hipantio 10-12 mm. longo.)

Type, Sanderson, Terrell Co., Texas, Mayl, 1934, *Cory* 8469, Pomona College Herbarium No. 200873. Known from a single collection.

10. *GAURA GRACILIS* Wooton & Standley, Contr. U. S. Nat. Herb. 16: 153. 1913.

Apparently biennial to short-lived perennial, branched at base, bushy, the stems slender, often reddish, hirsute or villous, simple or usually branched, ascending, 4-9 dm. high; basal leaves oblanceolate, sinuate-dentate, 4-10 cm. long, villous especially on margins and veins, with short winged petioles; cauline leaves rather numerous, linear or linear-oblong, entire to repand-toothed, more or less wavy, glabrous to stiff-pubescent, mostly 1-4 cm. long, 1-3 mm. wide, subsessile to very short-petioled, acute to obtuse; bracts of inflorescence ovate, acute to acuminate, ciliolate, 1-2 mm. long; spikes slender, simple or few-branched, relatively few-flowered, becoming 5-20 cm. long in fruit, on peduncles 5-15 cm. long; hypanthium reddish, slender, 5-7 mm. long, pubescent within; sepals reddish, linear, 4-5 mm. long, separate in anthesis; petals white to reddish, oblanceolate, 5-6 mm. long; stamens subequal, the filaments somewhat flattened, 4-5 mm. long; anthers reddish, ca. 2 mm. long; style exceeding stamens, pubescent at base, the stigma-lobes ca. 0.2 mm. long; capsule quite sessile or short-stipitate, ovoid-pyramidal, sharply 4-angled, mostly 4-6 (9) mm. long, and 2-2.5 mm. wide, glabrous, somewhat wrinkled transversely.

This species has been included in *G. suffulata*, but differs in its narrower cauline leaves, smaller flowers, and more western range at a higher altitude. It intergrades with *G. Nealleyi* to some extent through the forma *glandulosa*.

KEY TO VARIETIES

Calyx and hypanthium minutely strigillose to glabrous. . . . . 10. *G. gracilis* var. *typica*  
Calyx and hypanthium with short gland-tipped hairs. . . . . 10b. *G. gracilis* f. *glandulosa*

10a. *Gaura gracilis* Woot. and Standl. var. *typica* n.var.

*G. gracilis* Woot. & Standl., Contrib. U. S. Nat. Herb. 16: 153. 1913.  
*G. podocarpa* Woot. & Standl., l.c., 154. *G. strigillosa* Woot. & Standl., l.c.  
*G. brassicacea* Woot. & Standl., l.c., 152.

Hypanthium and calyx minutely strigillose to glabrous.

Type locality, Forest Nursery, Ft. Bayard, New Mexico. Range from Ariz. to western Texas and Durango. Representative material, ARIZONA:  $\frac{1}{2}$  mile west of Prescott, Yavapai Co., *Wolf* 2340 (G, P); Prescott, *Peebles*, *Harrison* & *Kearney* 8843 (G, P); Devils Canyon, Pinal Mts., *Kearney*



*Peebles & Harrison 3194* (Sac, US); Pine Canyon, Chiricahua Mts., *Blumer 1601* (G, NY, US); Santa Rita Mts., *Jones in 1903* (P); Garden Canyon, Huachuca Mts., *Harrison & Kearney 5798* (Sacaton, US). NEW MEXICO: Ft. Bayard Watershed, *Blumer 44*, type coll. *gracilis* (G, NY, US); Ruidoso Creek, White Mts., Lincoln Co., *Wooton in 1895*, type coll. *strigillosa* (US); Silver City, Grant Co., *Metcalfe 166*, type coll. *podocarpa* (G, NY, P, US); Socorro, *Vasey in 1881*, type *brassicacea* (US); Mimbres River, Black Range, Grant Co., *Metcalfe 1033* (G, NY, P, US); Pinos Altos Mts., *Greene in 1880* (G, NY, P). TEXAS: Rankin, Upton Co., *Cory 5136* (P); Converse, Bexar Co., *Wolff 980* (US). CHIHUAHUA: Chihuahua, *Palmer 204*, in 1908 (G, NY, US); near Pilaes, *Hartman 796* (G, NY, US); Soldier Canyon, Sierra Madre, *Jones in 1903* (P). DURANGO: La Providencia, *Nelson 4982* (US); Otinapa, *Palmer 552* (US); Durango, *Nelson 4619* (G, US).

The intergradation from a strigillose to a glabrous condition is so gradual and complete, as is that from a non-stipitate to a stipitate condition that I am unable to maintain the entities described by Wooton and Standley for recognition of these, such as *podocarpa*, *strigillosa*. I have not been quite so certain as to the status of *G. brassicacea* as of the others, and for that reason take up the name *gracilis* for this concept although *brassicacea* has page priority. I do agree with Wooton and Standley in maintaining this whole concept as a species distinct from *suffulta*. Their *glandulosa* seems to be a little more definite thing than the others, and yet, since it has no definite range or other characters, but is found growing with the typical form of the species, I am recognizing it as

10b. *Gaura gracilis* Woot. & Standl. forma *glandulosa* (Woot. & Standl.) n. comb.

*G. glandulosa* Woot. & Standl., Contrib. U. S. Nat. Herb. 16: 153. 1913. Hypanthium and calyx with short gland-tipped hairs.

Type locality, Reserve, Catron Co., New Mexico. Ranging with var. *typica*, Representative material, ARIZONA: 3 miles east of Flagstaff, *Munz 13002* (P); Willow Spring, *Rothrock 233* (G, US); Santa Catalina Mts., *Livingston & Thornber in 1906* (NY); Miller's Canyon, Huachuca Mts., *Goodding 250* (G, NY); Matzatzal Mts., *Collom* (NY, US). NEW MEXICO: White Mts., Lincoln Co., *Wooton 339* (NY, US); Reserve, *Wooton in 1906*, type coll. (US). CHIHUAHUA: Colonia Garcia, Sierra Madre, *Townsend & Barber 124* (G, NY, P, US); Sierra Madre, *Nelson 6110* (US).

There is considerable variation in fruit length (from 5-12 mm.), but I am unable to maintain any segregation by use of it.

(to be concluded)

# INDEX TO AMERICAN BOTANICAL LITERATURE

1934-1937

The aim of this Index is to include all current botanical literature written by Americans, published in America, or based upon American material; the word America being used in the broadest sense.

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- Airy-Shaw, H. K.** *Symplococarpon Hintoni* (Bullock) Airy-Shaw. Hooker's Icon. Plant 34: pl. 3342. S 1937.  
A new genus from Mexico.
- Albaum, H. G. & Kaiser, S.** The titration curves of 3-indole acetic, 3-indole propionic, and 3-indole butyric acids. Am. Jour. Bot. 24: 420-422. f. 1-3. J1 1937.
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## The vascular anatomy and comparative morphology of apocynaceous flowers

ROBERT E. WOODSON, JR., AND JOHN ADAM MOORE  
(WITH PLATES 3-5 AND 72 FIGURES)

Although systematic research in the anatomy of flowers dates from the classic investigations of Philippe Van Tieghem (1875) in the last quarter of the past century, the subject cannot be said to have attained prominence in the field of plant anatomy until approximately the past ten years. Within that period the lively discussions of floral anatomy which have been waged, particularly in England and the United States (Eames, 1931; Saunders, 1925) with respect to the merits or demerits of the polymorphic interpretation of crucifer carpels and those of other families of angiosperms has stimulated research concerning the general vascular structure of the flower in many of the important botanical laboratories of the world. Since the flower has been the principal basis of classification of all modern systems of the flowering plants, it is not unnatural that those botanists whose great desire it is to approach ever closer an approximation of evolution have turned to the research of floral anatomy as a timely and promising means to that end.

When the senior author of these observations commenced the taxonomic study of Apocynaceae somewhat over ten years ago, the first papers concerning floral anatomy had just begun to issue from the laboratories of Professor Eames of Cornell University, shortly to be followed by those of Miss Saunders of Cambridge, England. Such approaches to the study of the flower appeared so attractive and significant that an investigation of the floral anatomy of Apocynaceae was immediately begun. From this beginning an account of the vascular anatomy of the genera *Apocynum* and *Nerium* was published in 1930. It was not until several years later that the writer chanced upon a previous and more general account of the floral anatomy of *Apocynum* by Grelot (1897), with which his views were in general agreement.

In the years that have intervened, flowering material of 39 genera and 60 species of Apocynaceae, representing all subdivisions of the family in its distribution in both hemispheres, has been obtained from living specimens in botanic gardens and in the field through the efforts of the senior author and numerous friends to whom he is greatly indebted. Herbarium specimens, although available for such studies within the natural limitations due to desiccation, were employed only in a few critical genera extremely difficult to obtain in the field, such as the polycarpellary genus

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*Pleiocarpa* of tropical Africa. In general, serial transverse and longitudinal sections approximately  $10\mu$  thick were prepared according to the familiar alcohol-xylol-paraffin schedule, and stained in crystal violet and erythrosin, or fast green and safranin.

During the academic year 1935-36 the senior author of these observations was aided by the technical services of his former student, Dr. John Adam Moore, through a grant of the Science Research Fund of Washington University (St. Louis) provided by the Rockefeller Foundation.

#### REPRESENTATION OF GENERA AND SPECIES

Names preceded by an asterisk (\*) denote material obtained from herbarium specimens; all others obtained fresh, and fixed in formalin-acetic-alcohol.

#### Subfamily PLUMERIOIDEAE

*Acocanthera spectabilis* Hook.

*Allamanda cathartica* L.

*Amsonia ciliata* Walt.

*Carissa Carandas* L.

*C. grandiflora* A. DC.

*Cerbera Tanghin* Hook.

\**Cufodontia Stegomeris* Woods.

*Haplophyton cimicidum* A. DC.

*Lacmellia edulis* Karst.

*Lochnera rosea* (L.) Reichb.

\**Pleiocarpa bicarpellata* Stapf

\**P. mutica* Hook.

*Plumeria rubra* L.

*Plumeriopsis Ahouai* (L.) Rusby & Woods.

*Rauwolfia tetraphylla* L.

*Rhazya orientalis* (Dcne.) A. DC.

*Stemmadenia Alfari* (Donn. Sm.) Woods.

*S. grandiflora* (Jacq.) Miers

*S. obovata* (Hook. & Arn.) K. Sch.

*Tabernaemontana acutissima* Muell.-Arg.

*T. arborea* Rose

*T. chrysocarpa* Blake

*T. Cumingiana* A. DC.

*T. divaricata* R. Br.

*Thevetia peruviana* (Pers.) K. Sch.

*Vinca major* L.

*V. minor* L.

*Zschokkea panamensis* Woods.

*Z. ramosissima* Muel.-Arg.



## Subfamily ECHITOIDEAE

- Adenium coetanium* Stapf  
*Baumontia grandiflora* Wall.  
*Cycladenia humilis* Benth.  
*Forsteronia viridescens* Blake  
*Funtumia elastica* (Preuss) Stapf  
*Macrosiphonia Brachysiphon* (Torr.) Gray  
*M. Macrosiphon* (Torr.) Heller  
*Malouetia guatemalensis* (Muell.-Arg.) Standl.  
*Mandevilla Bridgesii* (Muell.-Arg.) Woods.  
*M. hirsuta* (A. Rich.) K. Sch.  
*M. illustris* (Vell.) Woods.  
*M. laxa* (R. & P.) Woods.  
*Mascarenhasia elastica* K. Sch.  
*Mesechites trifida* (Jacq.) Muell.-Arg.  
*Nerium Oleander* L.  
*Odontadenia Hoffmannseggiana* (Steud.) Woods.  
*O. Schippii* Woods.  
*Prestonia acutifolia* (Benth.) K. Sch.  
*P. portobellensis* (Beurl.) Woods.  
*Rhabdadenia biflora* (Jacq.) Muell.-Arg.  
*Strophanthus dichotomus* A. DC.  
*S. gratus* A. DC.  
*S. sarmentosus* A. DC.  
\**Thenardia Galeottiana* Baill.  
*Trachelospermum difforme* (Walt.) Gray  
*T. jasminoides* (Lindl.) Lem.  
*Urechites Andrieuxii* Muell.-Arg.

## Subfamily APOCYNOIDAE

- Apocynum androsaemifolium* L.  
*A. cannabinum* L.  
*Trachomitum venetum* (L.) Woods.

## GENERAL MORPHOLOGY OF THE FLOWER

The apocynaceous flower is always tetracyclic, and is pentamerous save in three small tetramerous genera. The calyx is barely gamosepalous in the majority of instances, the lobes being cleft nearly to the receptacle. The aestivation is almost invariably imbricated. The chief interest in the calyx of Apocynaceae lies in the frequent presence of small, glandular processes, known as "squamellae," which are found within, at the base of the lobes (cf. figs. 2, 5, 8).

The corolla is gamopetalous and actinomorphic throughout the family, and displays a wide assortment of campanulate, salverform, infundibuli-



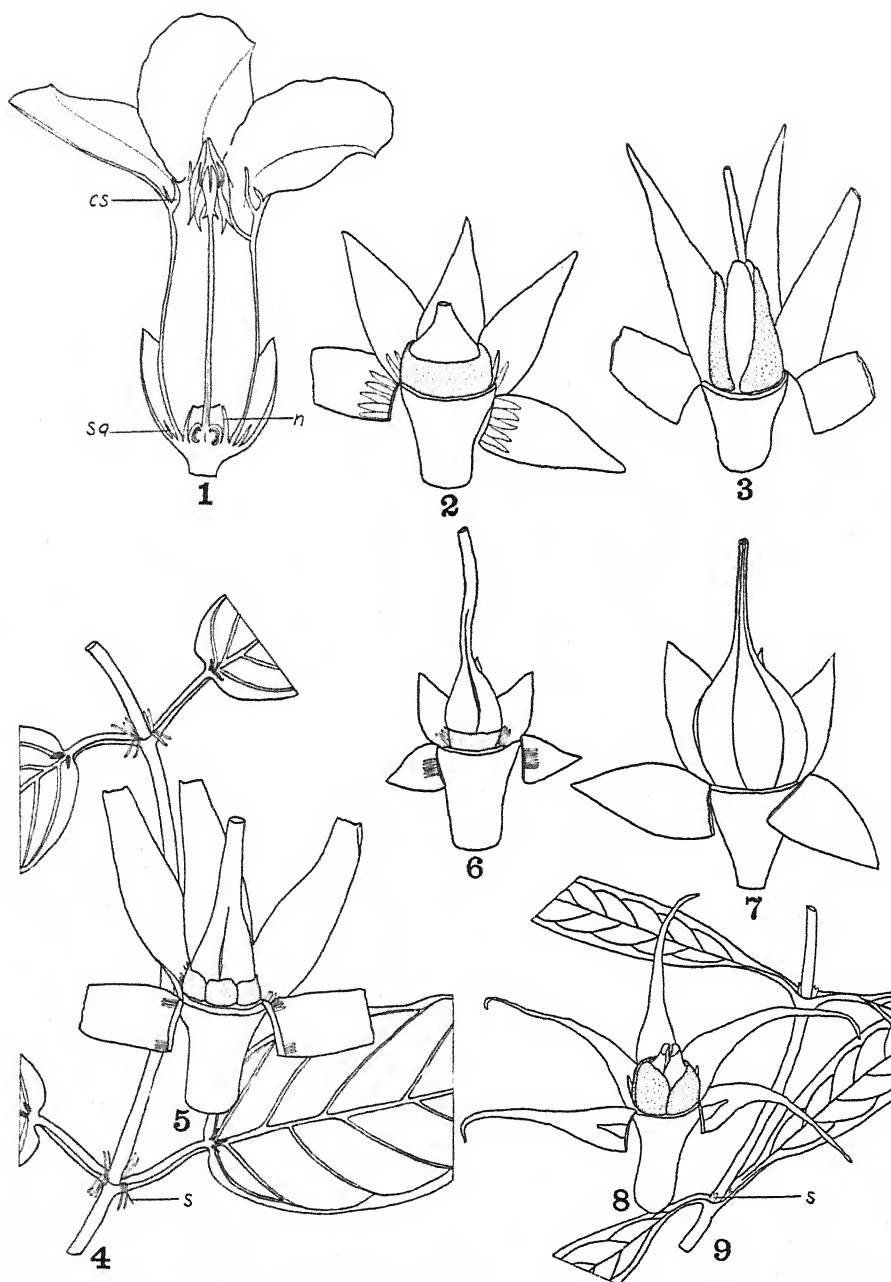
form, and rotate modifications. The aestivation is contorted. As in the calyx, the chief interest in the corolla is found in the occasional genera which bear various internal appendages, known as "corolline scales," which form structures strongly reminiscent of the corolline coronas of many Asclepiadaceae (cf. figs. 22, 23, 24). In certain genera, as *Strophanthus* and *Nerium*, the corolline scales may be conspicuously exerted and petaloid, while in others, as *Apocynum*, they may constitute exceedingly inconspicuous, basal emergences which may be observed only after dissection.

The stamens of Apocynaceae are always epipetalous and alternate with the corolline members. Although exceedingly diversified in their morphology and histology, the stamens offer little of interest from the standpoint of vascular anatomy. Nevertheless, the construction and relationship of the anthers has been found extremely practical in the separation of subfamilies: The Plumerioideae are distinguished by anthers without sterile, basal appendages and are not connivent nor agglutinated to the stigma; both the Echitoideae and the Apocynoideae have basally appendiculate anthers which are usually connivent and agglutinated to the stigma through the secretion of certain peculiar, glandular cells. The unique relation of the anthers and stigmata of Echitoideae and Apocynoideae has prompted the suggestion that those families may be more "advanced" than the Plumerioideae, perhaps representing a transition to Asclepiadaceae (Demeter, 1922). Such considerations, however, are without the scope of these studies which are concerned chiefly with vascular anatomy and interpretive gross morphology.

The ovary of Apocynaceae may be either apocarpous or syncarpous. When apocarpous, the ovary is usually bicarpellary, each carpel being infolded at the margins to form an axile, binate placenta. The two free carpels converge at the tips to form a common stylar shaft surmounted by a common, usually rather massive stigma (cf. fig. 1; pl. 5, fig. 6). Among the Apocynaceae with apocarpous ovaries are found a group of three or four genera, designated as the tribe Pleiocarpeae, which are characterized by as many as five free carpels. In such polycarpellary gynoecea each carpel contributes directly to the style and stigma (cf. fig. 7).

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Figs. 1-9. Fig. 1., longitudinal section, flower of *Prestonia portobellensis*: sq—squamella, n—nectary, cs—corolla scales; fig. 2, calyx and gynoeceum of *Thevetia peruviana*; fig. 3, calyx and gynoeceum of *Lochnera rosea*; fig. 4, vegetative branch of *Mandevilla Bridgesii*: s—stipular appendages; fig. 5, calyx and gynoeceum of *Mandevilla Bridgesii*; fig. 6, calyx and gynoeceum of *Tabernaemontana chrysocarpa*; fig. 7, calyx and gynoeceum of *Pleiocarpa mutica*; fig. 8, calyx and gynoeceum of *Thenardia Galeottiana*; fig. 9, vegetative branch of *Thenardia Galeottiana*: s—stipular appendages.



Among the syncarpous Apocynaceae both bilocular and unilocular bicarpellary ovaries are encountered. In the bilocular, the placentation of each cavity is axile and binate; in the unilocular ovaries are found two opposed, linear, parietal placentae (cf. pl. 5, figs. 1, 2). In either event the ovary is characterized by a common stylar shaft surmounted by the stigma in the usual manner for the family.

From the standpoint of these investigations, the chief interest in the gynoecium of Apocynaceae is found in the cycle of "nectaries" or "disc lobes" which surrounds the ovaries of many genera. These structures are usually more or less fleshy, and adopt a variety of modifications: chiefly as clusters of discrete bodies, two to five in number (cf. figs. 3, 5), or as collar-like or sleeve-like rings of tissue (cf. figs. 2, 6), about the base of the ovary. Although smaller than the carpels which they surround in most cases, the nectaries occasionally simulate the carpels not only in general shape, but in size as well. Although they frequently are more or less adnate to the ovary, they are always free from the style.

Although appearing to be quite superior in ordinary dissections, the ovaries of many Apocynaceae are more or less "subinferior," or immersed for a short distance within the receptacle. In the genera *Plumeria* (pl. 5, fig. 5) and *Himatanthus* this immersion is found to a marked degree, almost rendering the gynoecium completely inferior.

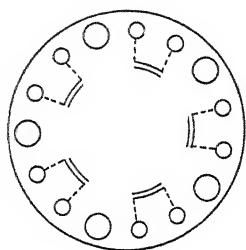
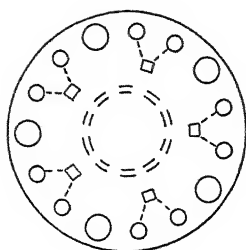
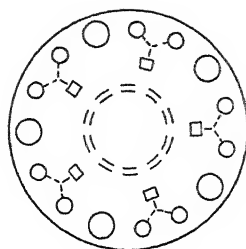
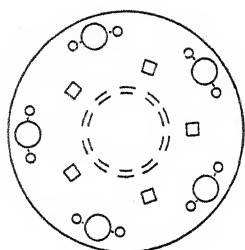
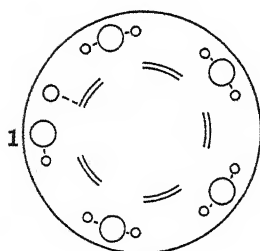
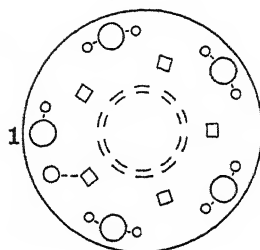
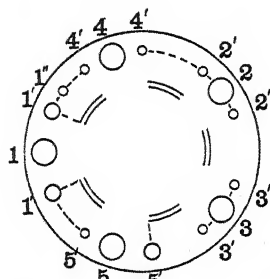
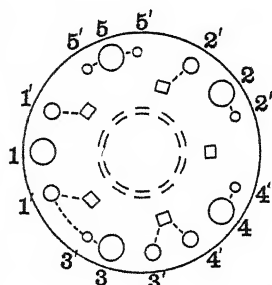
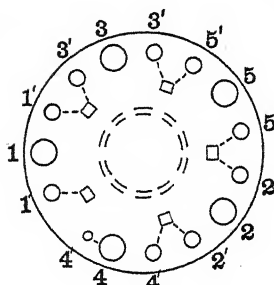
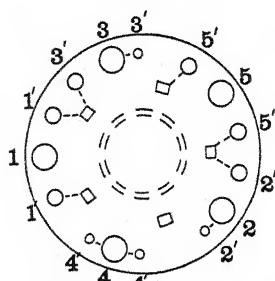
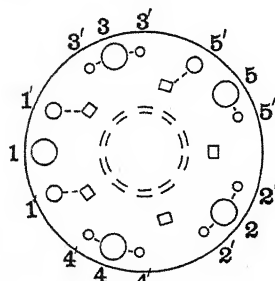
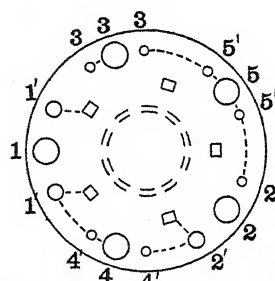
In order to avoid needless repetition, observations on the floral anatomy of the genera and species will be considered, not separately, but under headings of the various component structural units, such as pedicel, calyx, corolla and androecium, and gynoecium. This method not only is convenient but is justifiable since the flower, considered anatomically, is a condensed short shoot system bearing at the nodes appendages of differing structural and functional modifications.

#### ANATOMY OF THE PEDICEL

The pedicel of all known Apocynaceae contains an amphiphloic siphonostele (pl. 3, fig. 1) agreeing in general with that of the young stem. The internal phloem of certain genera demonstrates in the pedicel and receptacular stele a marked tendency to separate into small strands which leave the inner face of the protoxylem, from which they are frequently

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Figs. 10-21. Calyx anatomy of various Apocynaceae: calyx midribs indicated by large circles, calyx laterals by smaller circles, corolla midribs by squares, residual stele by double arcs, derivation of traces by broken single lines, centripetal succession of calyx lobes by numerals: fig. 10, *Lacmellia edulis*; figs. 11-12, *Mandevilla subsagittata*; figs. 13-14, *Mandevilla hirsuta*; fig. 15, *Tabernaemontana chrysocarpa*; fig. 16, *Thevetia peruviana*; figs. 17-21, *Rauwolfia tetraphylla*.

**10****11****12****13****14****15****16****17****18****19****20****21**

isolated by a few cells of basic parenchyma, and invade the pith, where they branch and anastomose irregularly (pl. 3, figs. 1, 2) as described by Scott and Brebner (1891) for the stems or roots of certain Gentianaceae, Apocynaceae, Asclepiadaceae, Solanaceae and Plumbaginaceae. In the apocynaceous flowers which we have investigated, it may be observed usually that the invasion of the pith by strands of internal phloem is perhaps most accentuated immediately before the departure of the calycine traces, after which the former are eliminated either by recombination with the normal internal phloem or by passage and combination outward with the traces to the calyx.

The internal phloem of apocynaceous flowers apparently consists chiefly of protophloem parenchyma, with but few poorly developed sieve tubes. The parenchyma is so similar in appearance to poorly developed provascular tissue that it scarcely comes as a surprise to find that in some cases it may behave similarly to the latter in differentiating into isolated, spiral tracheids (pl. 3, fig. 2). This phenomenon has been found in the pedicels not only of such Apocynaceae as *Tabernaemontana acutissima*, *Stemmadenia grandiflora*, and *Odontadenia Schippii*, but occasionally in certain gentianaceous flowers as well. The provascular tendency of the internal phloem of the pedicellar stele is quite probably to be correlated with the appearance of "meristems producing secondary, medullary wood" discovered by Scott and Brebner (1891) in the stems of *Apocynum cannabinum* L., *Willughbeia firma* Bl. (Apocynaceae), and *Periploca graeca* L. (Asclepiadaceae).

Similar to the internal phloem, the external phloem evidently consists principally of parenchyma in the pedicel. The outer is more uniform than the inner, however, and maintains its position immediately external to the xylem.

The pedicellar wood consists chiefly of protoxylem with a relatively scant development of metaxylem and secondary xylem. Vessels apparently are never present, and the secondary walls of the tracheids are either spiral or annular. Fibers never occur such as have been found in the flowers of certain Gentianaceae (Woodson, 1936).

The organization of latex tissues within the pedicel, as within the flower as a whole, is extremely diversified, to such an extent that observations concerning the laticiferous, storage, and secretory systems will be ignored in this account, possibly to be treated more fully in a subsequent paper.

#### VASCULAR ANATOMY OF THE CALYX

In the lower receptacle of all apocynaceous flowers the pedicellar stele, usually roughly circular in outline at first, becomes more or less sharply

5- or 10-lobed. In the former case, the lobes are identical with the decurrent midribs of the five calyx lobes. Alternating with these five lobes, the five additional in the 10-lobed stele indicate in most instances the positions of the corolline midribs (cf. fig. 53). As one would expect, the first series of traces to depart from the pedicellar stele are those destined to supply the calyx. For general purposes the calyces of all known Apocynaceae may be divided into four types of organization with respect to their nodal anatomy:

*Type I.* In the calyces included under Type I the midribs depart from the receptacular stele leaving in each case a single gap. Then, before the stele has again united, the margins of the five gaps give off a single trace, ten in all, which are the lateral traces of the calyx lobes (fig. 10). These lateral traces are therefore coherent to the margins of the gaps left in the stele by the departure of the calyx midribs, and the nodal anatomy in each case is essentially a 3-trace, 1-gap system. Both midrib and laterals soon give rise to small subsidiary veinlets of decreasing magnitude as they progress toward the tips of the calyx lobes.

Various modifications of the typically symmetrical nodal anatomy obtain, frequently in different flowers from the same inflorescence. For example, the lateral traces of each calyx lobe may depart from the receptacular stele to which they are coherent somewhat before the departure of the midribs. Occasionally one margin of the gap left by a midrib may produce no lateral trace, giving rise to a 2-trace condition which may proceed to the tip of the calyx lobe.

The condition of this type may be recognized as basically 3-trace, 1-gap, with the laterals coherent separately to the margins of the midrib gaps *before the organization of the corolline traces*. It appears probable, in view of the widespread opinion that the 3-trace condition is primitive for both vegetative and floral appendages (Sinnott, 1914; Eames, 1931), that the apocynaceous calyces included within Type I are the most "primitive" from the structural standpoint. It is interesting to note in this connection that the vegetative nodes of all known Apocynaceae produce a single trace from which the laterals are subsequently derived.

Genera and species showing various modifications of the Type I calyx vascular skeleton include:

*Lacmellia edulis* Karst.

*Malouetia guatemalensis* (Muell.-Arg.) Standl.

*Stemmadenia Alfari* (Rose) Woods.

*S. grandiflora* (Jacq.) Miers

*S. obovata* (Hook. & Arn.) K. Sch.

*Tabernaemontana acutissima* Muell.-Arg.

*T. arborea* Rose.



Features of vascular organization in varying extents similar to Type I, but which are asymmetrically combined with other types, will be discussed under Type IV. It may be of phylogenetic significance that all the genera enumerated above are referable to the subfamily Plumerioideae, save *Malouetia*, which is ordinarily included within the Echitoideae although it was placed in an intermediate position by Mueller (1860).

*Type II.* The second type of calyx, with respect to vascular anatomy, includes those species in which the lateral traces of the lobes are adnate to the base of the corolline midribs. In this type, the departure of the calyx midribs is immediately followed by the organization of the five midribs to the corolla lobes. Soon after the differentiation of the corolline midribs from the receptacular stele, the adnation of the calyx laterals is terminated, and either the two laterals of adjacent calyx lobes depart separately from the single, alternate corolla midrib (fig. 11), or the two cohere mutually for a short distance after their common severance from the corolline trace (fig. 12). When the calyx laterals are adnate separately to the corolline midrib or cohere mutually for a short distance appears relatively insignificant, as the two conditions may be found usually in the same species, if more than one specimen be examined.

Type II is significant, however, in so far as the 3-trace condition found in Type I evidently is more elaborate, progressing from cohesion to the receptacular stele proper to adnation to the corolla midrib. Genera and species illustrating various modifications of the Type II calyx skeleton include:

- Amsonia ciliata* Walt.
- Carissa Carandas* L.
- C. grandiflora* A. DC.
- Forsteronia viridescens* Blake
- Funtumia elastica* (Preuss) Stapf
- Haplophytum cimicidum* A. DC.
- Lochnera rosea* (L.) Reichb.
- Mandevilla subsagittata* (R. & P.) Woods.
- Rhabdadenia biflora* (Jacq.) Muell.-Arg.
- Rhazya orientalis* (Dcne.) A. DC.
- Tabernaemontana Cumingiana* A. DC.
- T. divaricata* R.Br.
- Thenardia Galeottiana* Baill.
- Trachelospermum difforme* (Walt.) Gray
- T. jasminoides* (Lindl.) Lem.
- Urechites Andrieuxii* Muell.-Arg.
- Vinca major* L.
- V. minor* L.



If this enumeration is compared with the classification of the Apocynaceae studied during this investigation (p. 136), it will be seen that the genera included above are referable to both subfamilies Plumeroideae and Echitoideae in equal proportions.

*Type III.* The simplest type of vascular anatomy found in apocynaceous calyces is found in Type III, in which each calyx lobe is strictly 1-trace. This midrib departs from the receptacular stele quite regularly, later giving rise to laterals upon either side, in a manner which is predominant amongst the majority of Gamopetalae (fig. 13). This simple calyx skeleton is found throughout the various taxonomic divisions of the Apocynaceae, and is quite possibly more "advanced" phylogenetically than either Type I or Type II. Genera and species illustrating this type include:

*Adenium coeternium* Stapf  
*Allamanda cathartica* L.  
*Apocynum androsaemifolium* L.  
*A. cannabinum* L.  
*Cerbera Tanghin* Hook.  
*Cycladenia humilis* Benth.  
*Mandevilla hirsuta* (A. Rich.) K. Sch.  
*M. illustris* (Vell.) Woods.  
*M. splendens* (Hook.) Woods.  
*Meschites trifida* (Jacq.) Muell.-Arg.  
*Nerium Oleander* L.  
*Pleiocarpa bicarpellata* Stapf  
*P. mutica* Benth.  
*Plumeria rubra* L.  
*Plumeriopsis Ahouai* (L.) Rusby & Woods.  
*Prestonia acutifolia* Benth.  
*P. portobellensis* (Beurl.) Woods.  
*Strophanthus dichotomus* A. DC.  
*S. gratus* A. DC.  
*S. sarmentosus* A. DC.  
*Tabernaemontana chrysocarpa* Blake  
*Trachomitum venetum* (L.) Woods.

Even this type is not entirely free from variation, however, since occasionally a single lateral is found to proceed from either the margin of the gap left in the receptacular stele by the departing calyx midrib (fig. 14) as in Type I, or from the corolline midrib (fig. 15) as in Type II.

*Type IV.* For the purpose of exposition, Type IV is most easily considered after the three preceding types. Actually, however, it is intermediate between all three, incorporating features of Types I and III, or

of Types II and III. In this type of calyx skeleton the vascular supply to the five lobes is distinctly asymmetrical, certain of the lobes receiving their traces according to Type I or Type II, and the others according to Type III. Something of phylogenetic value may be adduced from the fact that the outer lobes are more prone to Types I or II than are the inner, which are somewhat more likely to show Type III (figs. 16-21 inclusive).

The impetus to this condition may be the strong imbrication of the calyx lobes of many genera and species, the inner frequently being more or less completely enclosed within the outer, the two series becoming somewhat different in appearance. This tendency is well marked in the genus *Odontadenia*, and culminates in the remarkable calyx of *Cufodontia*, unparalleled amongst known Apocynaceae (in which the two or three outer lobes become connate, completely hiding the smaller pair within).

Genera and species showing various modifications of the Type IV calyx skeleton include:

(Combination of Types I and III)

- Beaumontia grandiflora* Wall.
- Macrosiphonia Brachysiphon* (Torr.) Gray
- Mascarenhasia elastica* K. Sch.
- Odontadenia Hoffmannseggiana* (Steud.) Woods.
- O. Schippii* Woods.
- Thevetia peruviana* (Pers.) K. Sch.
- Zchokkea panamensis* Woods.
- Z. ramosissima* Muell.-Arg.

(Combination of Types II and III)

- Mandevilla Bridgesii* (Muell.-Arg.) Woods.
- M. laxa* (R. & P.) Woods.
- Rauwolfia tetraphylla* L.

The vagaries of this type may be illustrated best by a few individual species, considering a single flower for each. For, as will be shown in the case of *Rauwolfia tetraphylla*, one may obtain almost any conceivable mixture of the types by examining a number of flowers from a single inflorescence.

*Thevetia peruviana* (fig. 16). Outermost calyx lobe (1)<sup>1</sup> similar to Type I, with the laterals cohering to the margins of the midrib gap, but each lateral branching within the receptacle to form the adjacent laterals of the neighboring lobes (4-5). Of the remaining lobes, two (2-3) are essentially like Type III, giving rise to their own laterals, but in the case of one of

<sup>1</sup> The parenthetical numerals refer to the succession of lobes as visualized in the ideographs, progressing centripetally, from 1 to 5.

these (2), one forks to give rise to the lateral of the lobe to the left (4), similarly to the type of cohesion seen in the outermost lobe (1). In the case of the innermost lobe (5) one lateral is produced from the adjacent lateral of the outermost lobe, while the other coheres to the margin of the midrib gap according to the situation found in Type I. In this flower of *Thevetia*, therefore, an odd mixture of Types I and III exists in addition to three puzzling instances of cohesion of adjacent laterals of neighboring lobes.

*Rawwolfia tetraphylla* (figs. 17-21 inclusive). The variation shown in calyces of the Type IV vascular system is well shown in *Rawwolfia tetraphylla*. From a single inflorescence of this species preserved in alcohol for the senior writer by the late Dr. N. L. Britton upon his last trip to Puerto Rico, twelve flowers were selected for comparison. Each of these twelve calyces demonstrated a different combination of Types II and III, together with cohesions similar to those found in *Thevetia peruviana*.

Five variations of the calyx skeleton of this species are diagrammed in figures 17-21 inclusive. In figure 17 a peculiar cohesion is illustrated involving the right (as seen from within) lateral of lobe 1, with the left lateral and the midrib itself of the adjacent lobe 3. A precisely similar cohesion is found in figure 21 involving lobes 1 and 4; furthermore this skeleton is complicated by cohesions involving the adjacent right and left laterals of lobes 2 and 4 respectively, while the laterals of lobe 5 are both coherent to the laterals of adjacent lobes 3 and 2.

The striking variability of the calyx anatomy of Type IV genera and species is somewhat of a deterrent to the direct correlation of vegetative and floral nodal anatomy. At the same time, an impetus should be given to the study of variation in floral anatomy, a field that has appeared to at least some observers to be in imminent danger of "too easy" interpretations. On the other hand, the derivation of the 1-trace from the basic 3-trace condition is decidedly clarified by the very existence of transitions.

#### THE NATURE OF THE CALYCINE SQUAMELLAE

The most interesting feature of the apocynaceous calyx from the standpoint of comparative morphology is the occurrence of the internal glands, or "squamellae." The position, numbers, and aspect of these small structures are sufficiently constant and characteristic to be of importance taxonomically. There are three chief categories of squamellae with respect to their relationships with the calyx lobes which they subtend: *alternate* with the lobes, upon the margins of which they appear to be attached, either singly or in groups (fig. 5), *opposite* the lobes, solitary (fig. 8) or

in groups (fig. 6), or *indefinitely distributed*, when they seem to form a fringe of many individuals uniformly distributed around the very base of the calyx (fig. 2). Although squamellae are frequent in the family, they are occasionally lacking (figs. 3, 7).

It is significant to note that the vegetative nodes of most Apocynaceae also bear small, frequently glandular structures at the base of the petioles. As in the squamellae, these nodal appendages may be either alternate, opposite, or indefinitely distributed with respect to the petiole. Although the Apocynaceae are usually considered as an exstipulate family, these appendages are doubtless in the category of stipules, following the interpretation of Glück (1919). As one studies the Apocynaceae, one cannot fail to observe the fact that the position of the squamellae with respect to the calyx lobe is in most cases quite similar to that of the appendages of the vegetative node with respect to the petiole (cf. figs. 4, 5; 8, 9). One would be justified in assuming from this evidence the two categories to be equivalent, and the calycine squamellae as stipules.

This observation upon gross morphology is substantiated materially by studies of microscopic anatomy. As seen in longitudinal (pl. 3, fig. 7) or transverse section (pl. 4, fig. 6), the squamellae are found to consist of a small core of somewhat elongated cells continuous with the mesophyll of the calyx lobe which they subtend, surrounded by a glandular epidermis of horizontally compressed cells usually containing a nucleus in the region nearest the "core." Vascular tissue usually is lacking, but in such species as *Strophanthus gratus* (pl. 4, fig. 6) and *Funtumia elastica* (pl. 4, fig. 5) small bicollateral bundles derived from the marginal venation of the calyx lobe are found to be present, simulating the vascular supply of many stipules (Sinnott and Bailey, 1914). Both from the standpoint of gross morphology and from the vascular anatomy of certain species, therefore, the stipular nature of the squamellae appears well substantiated.

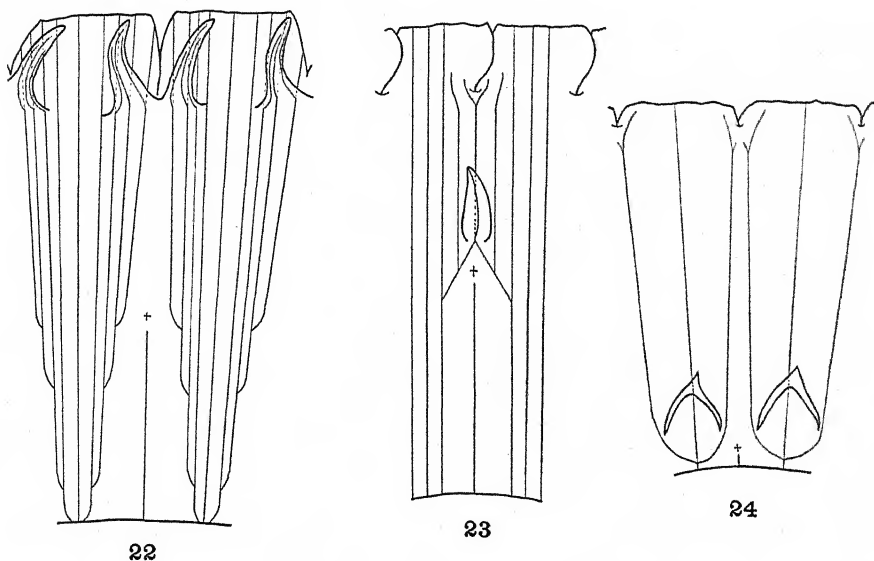
As in the case of normal, marginal stipules, the alternate type of squamellae would appear basic. The solitary, opposite squamella would appear to have been derived by the fusion of two marginal squamellae in a position adaxial to the calyx lobe which they subtend. Evidence to support this assumption is found in serial sections of such a flower as that of *Mandevilla subsagittata* (pl. 4, figs. 3-4), in which the very base of the opposite squamella is found to be bipartite and related to the margins of the calyx lobe. The indefinitely distributed squamellae are explainable with justification merely by assuming the developmental laceration of either alternate or opposite members.

The foliar nature of the calycine squamellae of Apocynaceae therefore appears fairly obvious, according to Glück's (1919) observations from

gross morphology, and in contradiction to Woodson's (1930) previous interpretation of these organs as possibly staminodia, a position, adopted entirely upon the basis of adenopetaly in double flowers of *Nerium Oleander*, which must now be discarded.

#### VASCULAR ANATOMY OF COROLLA AND ANDROECIUM

The nodal anatomy of the corolla of Apocynaceae is relatively simple. To each of the normally five lobes of the gamopetalous corolla a single trace departs from the receptacular stele after the differentiation of the calycine midribs. Almost at the same time five alternate traces are produced for the five epipetalous stamens. An exception to this general con-



Figs. 22-24. Morphology and vascular anatomy of the corolla scales of certain Apocynaceae: fig. 22, *Strophanthus sarmentosus*; figs. 23, *Prestonia portobellensis*; fig. 24, *Apocynum androsaemifolium*. The point of attachment of stamens is indicated as +

dition is found in the investigated species of *Apocynum* and *Trachomitum* (figs. 53-57 inclusive), both members of the subfamily Apocynoideae, in which the staminal traces are briefly adnate to the midribs of the opposite calyx lobes.

The chief feature of interest as far as the general vascular anatomy of the corolla is concerned is the adnation of the calyx laterals to the corolline midribs in certain genera and species, which already has been discussed. Lateral venation is obtained in the corolla merely by the more or less



frequent branching of the midrib. The staminal bundles remain unbranched throughout their adnation to the corolla as well as throughout the staminal filaments and the anthers.

The curious anatomy of the anthers is a topic of interest because of the extreme variation of cellular modification. Since this subject deals exclusively with modifications of the fundamental tissues, however, it will be deferred for the present, perhaps to be treated in a future paper on the reproductive mechanism of the family.

#### THE NATURE OF THE COROLLINE SCALES

The chief morphological interest in the corolla of Apocynaceae lies in the faucal appendages or "corolline scales" occasionally found within the gamopetalous tube. These appendages frequently are showy and laminate, forming a fringe or "corona" within the throat of the corolla from which they may be widely exerted. In such genera as *Strophanthus* (fig. 22) these scales occur in pairs alternate with the corolla lobes. In *Prestonia* (fig. 23) a single appendage occurs immediately above the insertion of the stamens. In *Apocynum* (fig. 24) they are inconspicuous and scale-like, and adnate to the base of the corolla tube and opposite the lobes.

The corolline scales of apocynaceous corollas apparently are never glandular, the organization of the fundamental tissues being in all essential respects similar to that of the corolla proper. Furthermore certain of the scales, such as those of *Apocynum* and *Trachomitum*, contain no vascular tissue, and one might be led to consider them simply as emergences of no particular morphological significance. In the majority of such appendaged corollas, however, the presence of well developed vascular tissues may be proved, and the skeletal relationship of the appendages and the corolla proper easily observed by clearing the whole corolla in lactic acid. Diagrams of segments of three representative corollas treated in this manner are provided in figures 22-24 inclusive.

*Strophanthus sarmentosus* (fig. 22) possesses paired faucal appendages alternate with the corolla lobes. In cleared corollas the vascular bundles traversing each appendage are found to be derived from the outermost lateral veins of the adjacent corolla lobe. Furthermore it is found that the traces entering the appendage are merely branches of the corolline laterals which proceed up into the corolla lobe. When compared with the gross morphology and vascular anatomy of such a stipulate node as that of *Pelargonium* (Sinnott and Bailey, 1914) it appears obvious that the corolline scales of *Strophanthus* must be interpreted as stipules.

An interesting modification of the corolline appendage is found in species of *Prestonia* (fig. 23), which is solitary and alternate with the

corolla lobes. In the case of *P. portobellensis* a single vascular strand is found within the scale. But this strand has been formed by the fusion of branches from the outermost lateral vein of both adjacent corolla lobes, the veins themselves continuing up into the respective corolla lobes. This condition is decidedly similar to that of the single interpetiolar stipules of many Rubiaceae. Far from being an "exstipulate family," therefore, the Apocynaceae are seen to bear stipules not only at the vegetative nodes, but subtending the members of both calyx and corolla as well. Both the calyx and the corolla of this family are evidently foliar.

#### VASCULAR ANATOMY AND COMPARATIVE MORPHOLOGY OF THE GYNOECEIUM

The gynoecium of Apocynaceae is more diversified than is generally understood. Normally it is bicarpellary, the ovary proper being apocarpous or syncarpous. When apocarpous, each carpel possesses an infolded, marginal placenta bearing few to numerous ovules. When syncarpous, the component carpels may adhere more or less closely by their commisural margins, but maintaining their individuality to create a bilocular ovary, each loculus containing an axile, binate placenta similar to that found in apocarpous ovaries (pl. 5, fig. 1).

When unilocular, however, the ovary contains two parietal placentae oriented horizontally to the position of the two axile placentae of the bicarpellary ovary (pl. 5, fig. 2). In frequent instances one finds that a syncarpous ovary is bilocular at both base and apex, where placentation is axile, but unilocular in the middle where placentation is parietal. The natural inference from such a simple observation is that the unilocular condition has been derived from the bilocular phylogenetically as well as ontogenetically, by the cohesion of contiguous placental margins of the component carpels, and the separation of the component halves of the erstwhile binate placentae. The simple process by which this coexistent cohesion and separation may be accomplished is obvious when one observes in bilocular, syncarpous ovaries that the closely appressed epidermal layers of the infolded margins composing the axile placentae of either carpel retain their distinction long after the epidermis separating the two carpels themselves has been obliterated.

Another proof of the two parietal placentae as consisting of fused halves of adjacent axile placentae is found in the orientation of the vascular bundles contained within the common stylar shaft uniting the carpels. The styles of bicarpellary Apocynaceae invariably contain two separate bundles which are the prolongations of the respective carpellary midribs. In the styles of bilocular ovaries the orientation of the bundles



is in the same diameter with respect to the axile placentae (cf. figs. 51–52; 71–72), but invariably at a deviation of roughly  $90^\circ$  with respect to the parietal placentae (cf. figs. 69–70). This simple observation should at once explain the derivation of parietal from axile placentae and confound the attempt to explain the “commisural stigma” upon the basis of “carpel polymorphism (Saunders, 1925).”

Although predominantly bicarpellary, the Apocynaceae include a few polycarpellary genera constituting the tribe Pleiocarpeae of the subfamily Plumerioideae. The number of carpels in this tribe varies from two to five, the whole range being encountered amongst different species of the single African genus *Pleiocarpa* (fig. 7). In some species of *Pleiocarpa* the number of fertile carpels tends to vary, as will be shown presently. The ovary of all polycarpellary genera always is apocarpous, but the component carpels are united by a rather poorly organized style within which the number of vascular bundles corresponds (cf. figs. 29, 33).

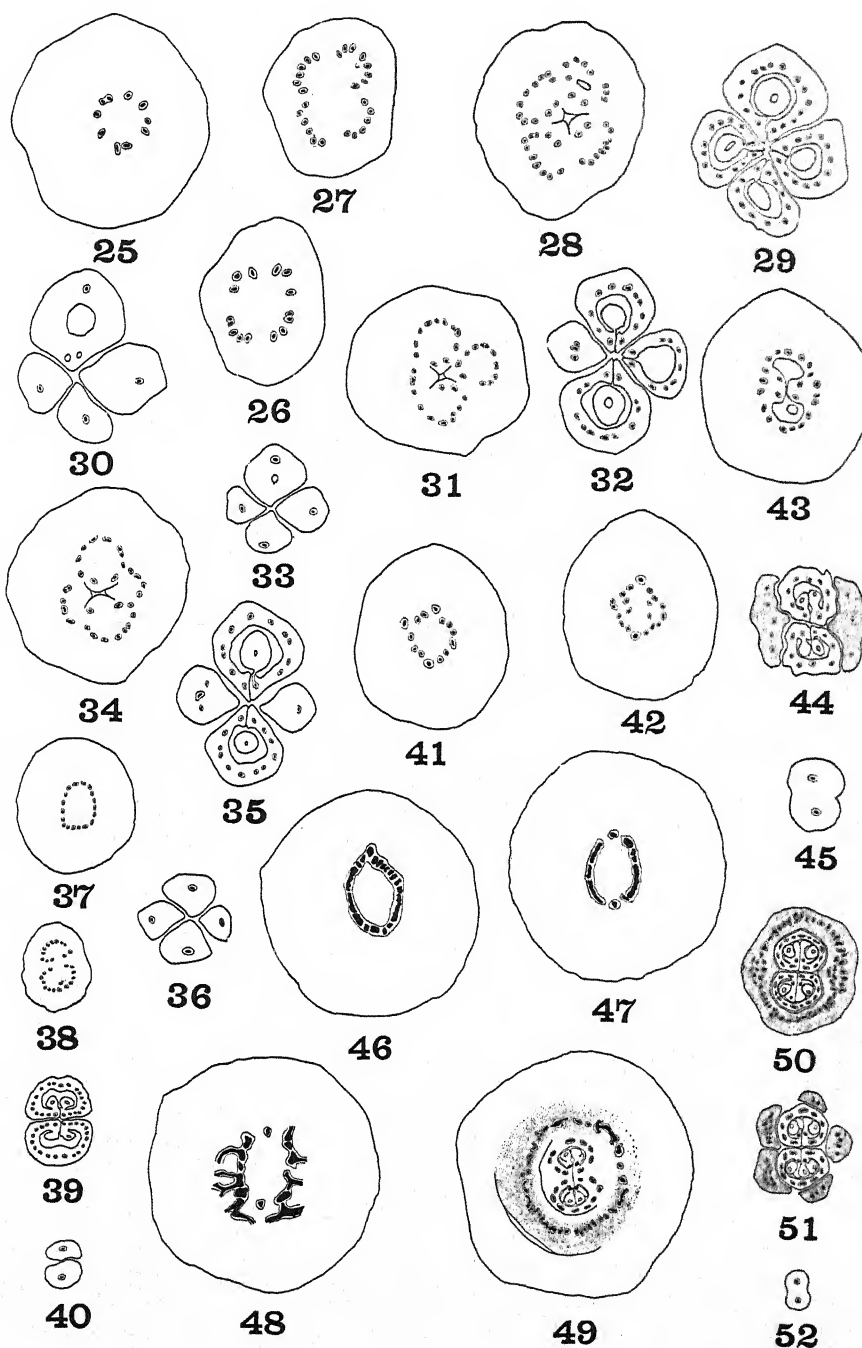
Surrounding the ovary of Apocynaceae one usually finds a cycle of fleshy bodies known as “nectaries” or “disc lobes.” The nectaries frequently are separate, and two to five in number (figs. 3, 5), but occasionally they cohere to form a nearly uniform, annular structure (figs. 1, 2, 6). Occasionally the nectaries are quite as massive as the carpels, which they simulate in general aspect save for the fact that they do not contribute to the style (figs. 3, 8).

That the nectaries definitely are appendages and not merely meaningless hypertrophies of the receptacle is demonstrated by the fact that they contain definite vascular tissue associated with that of the gynoecium proper. The fundamental tissue comprises an elaborate assortment of secretory and storage cells a comprehensive discussion of which is without the scope of this paper (cf. pl. 3, figs. 6, 7; pl. 5, fig. 3). After a study of the floral anatomy of *Apocynum*, Woodson (1930) concluded that the nectaries of Apocynaceae should be interpreted as carpelloses. That position may now be given support by a study of numerous additional genera, particularly the polycarpellary species *Pleiocarpa mutica*.

The vascular anatomy of the ovaries and associated nectaries of all genera and species studied during the present investigations may be treated by representative illustrations which follow.

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Figs. 25–52. Vascular anatomy of the gynoecium of Apocynaceae, traces to the perianth and stamens omitted. Explanation in the text. Figs. 25–36, *Pleiocarpa mutica*; figs. 37–40, *P. bicarpellata*; figs. 41–45, *Lochnera rosea*; figs. 46–52, *Mandevilla subsagittata*. In these diagrams glandular tissue pertaining to the nectaries is stippled.



*Pleiocarpa*

It has been impossible to obtain fresh material of the interesting genus *Pleiocarpa*. The genus is relatively poor in herbarium representation as well. However, three flowers were removed from a herbarium specimen of *P. mutica* Benth., and prepared in serial sections after softening in "diaphanol" according to a method outlined in a previous account by the senior writer (Woodson, 1935). It is interesting to observe that these flowers constituted a cymule, the first flower to be observed being the central member.

*Flower 1* (figs. 25-30 inclusive). After the departure of the perianth and stamen traces, the receptacular stele is found to consist of approximately 10 to 20 small bundles assuming a roughly circular orientation (fig. 25). Four adjacent pairs of these, situated at regular intervals within the stele, migrate toward the center, and are subsequently found to be the placental bundles of the four component carpels (figs. 26, 27). This interpretation shortly is proved by the appearance of ovary cavities and the subsequent separation of the carpels from the receptacle (figs. 28, 29). It is not until after the full organization of the carpels that the respective midribs become obviously distinct from the sessile secondary venation. In this flower all four carpels are hollow and fertile.<sup>2</sup>

*Flower 2* (figs. 31-33 inclusive). After the departure of the perianth and staminal bundles, the residual receptacular stele consists as in the first flower of about 10-20 bundles arranged in a circle. Two pairs of these migrate toward the center, but the remaining two pairs observed in the previous flower are represented merely by a single bundle for each, which likewise migrate centripetally (fig. 31). It is not surprising, therefore, to find that subsequent events produce but three hollow carpels, only two of which, incidentally, are ovuliferous. The fourth carpel of the first flower is replaced by a solid carpellode (fig. 32). Both the sterile carpel and the solid carpellode contribute their midribs to the style, however, and can scarcely be considered as precisely equivalent to "nectaries" (fig. 33).

*Flower 3* (figs. 34-36 inclusive). In this flower the residual stele of the receptacle consists, as before, of about 10-20 bundles. Four solitary, equidistant bundles migrate centripetally (fig. 34), and it is found subsequently that the ovary consists of two hollow, ovuliferous carpels alternating with two solid carpellodes which have been supplied by the arcs of bundles intervening between the pairs of placental traces (fig. 35). As in the second

<sup>2</sup> The use of the terms "hollow," "fertile," "sterile," and "solid" are used here strictly in a descriptive sense and without the specialized meanings of the writers on "carpel polymorphism" (Saunders, 1925).

flower, the carpellobes contribute their midribs to the style (fig. 36).

In the three flowers of a single cymule of *Pleiocarpa mutica*, therefore, a striking tendency to the reduction of the number of fertile carpels is found. In *P. bicarpellata* Stapf sections of several flowers have revealed but two (fertile) carpels in each case, and without any indication whatever of carpellody (cf. figs. 37-40 inclusive). The anatomy of these ovaries is essentially similar to that of *Cerbera Tanghin*, which will be explained subsequently.

### *Lochnera*

The two ovuliferous carpels of several genera and species of Apocynaceae alternate with as many fleshy nectaries. A good illustration of this condition is *Lochnera rosea* (figs. 41-45 inclusive). In this species, as in *Pleiocarpa mutica*, the residual stele of the receptacle consists of about 20 bundles. As in the third flower of *P. mutica* also (fig. 34), four equidistant bundles migrate centripetally to produce the placental bundles of the two ovuliferous carpels; the two arcs of bundles intervening supply the two alternating nectaries (figs. 42-44). These true nectaries differ from the solid carpellobes observed in the third flower of *Pleiocarpa mutica* only in so far as they do not contribute to the style (fig. 45). Nevertheless the true nectaries of *Lochnera* and the solid carpellobes of *Pleiocarpa* are almost exactly similar as far as their vascular origin is concerned, and their position also argues in favor of their relationship.

It appears obvious that the nectaries of *Lochnera* should be considered as carpellobes, and this interpretation extends itself to other nectaries of Apocynaceae. Other species possessing two nectaries of an anatomical organization essentially similar to that of *Lochnera rosea* include:

*Vinca major* L.

*V. minor* L.

### *Mandevilla*

The vascular organization of the ovary and nectaries of *Mandevilla subsagittata* (R. & P.) Woods. (figs. 46-52 inclusive) is representative of all investigated species of *Mandevilla* and several closely related genera. In this species the receptacular stele unites after the departure of the corolline and staminal traces, a rare phenomenon amongst the Apocynaceae that have been investigated (fig. 46). The stele is somewhat elliptical in section, and very shortly the midribs of the two carpels depart by gaps from the opposite, narrowed ends of the ellipse (fig. 47). Meanwhile, the two broad arcs of the stele branch outward into an aggregate of separate bundles (fig. 48). The stele is now completely disrupted into

bundles of varying size, but all smaller than the two opposed midribs which have remained unbranched.

Centripetal migration of four to eight bundles roughly equidistant from the midribs now takes place to form the lateral bundles of each carpel. The organization of the carpels and the nectaries now takes place with the peripheral residual bundles supplying the latter (figs. 49, 50). The nectaries of this species, which superficially appear to be five in number in ordinary dissections, are found to be united at the base. Very shortly after their organization from the receptacle and the gynoeceum proper, radial division of the bundles, occurring first in two planes alternate with the two carpels, produces something of a "polydesmic" condition, which is continued for a short space even after the organization of the five separate nectary lobes (figs. 50, 51).

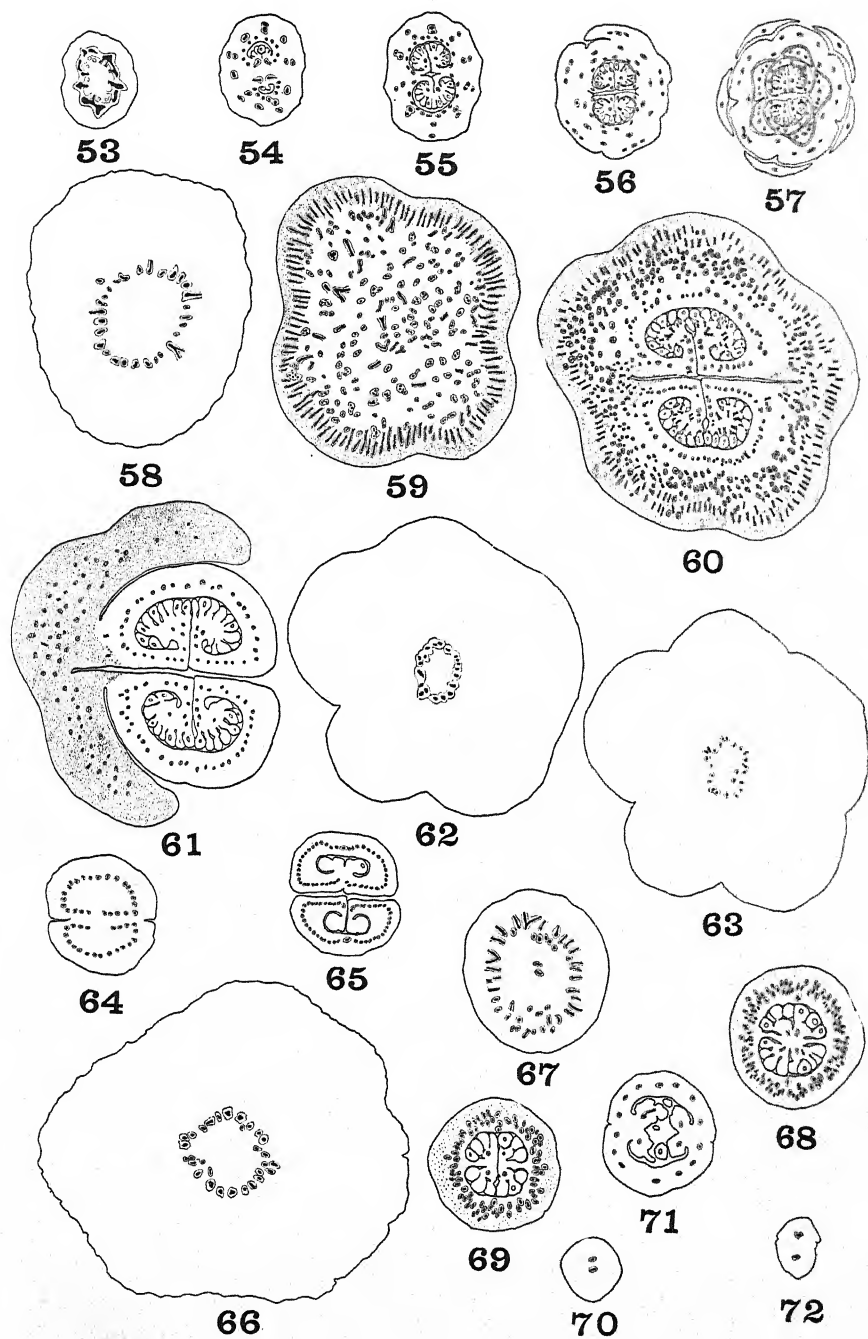
The nectaries of *M. subsagittata* and its congeners, as well as those of other genera having this type of gynoeceal anatomy, are usually five in number. But whether the gross aspect of the bodies should be taken as indicating the sterilization of five separate carpels, or whether the fact that the vascular supply of the cycle of nectaries has its origin in a somewhat similarly bilateral fashion to those of *Lochnera* is an indication that here also but two carpellodes are involved, is not wholly decided by the evidence, although the latter appears probable. Evidence to support the latter assumption may be found in the fact that only two nectary lobes are found in several species of *Mandevilla*, such as *M. splendens* (Hook.) Woods., and *M. illustris* (Vell.) Woods. The 5-lobed condition in *M. subsagittata* and other species might be interpreted as an instance of ontogenetic schizogeny due to internal pressures within the developing pentamorous flowers. The annular nectary of several species of *Odontadenia*, such as *O. Hoffmannseggiana* (Steud.) Woods. is cleft into almost innumerable tooth-like segments whose number is certainly not indicative of the number of carpellodes actually involved.

In any event, the vascular supply of the nectaries of *M. subsagittata* differs from that of *Lochnera* chiefly in its adnation to the lateral bundles of the carpels; and the nectaries here as well are evidently to be considered as carpellodes. Other genera and species having a gynoeceal skeleton similar to that of *M. subsagittata* include:

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Figs. 53-72. Vascular anatomy of the gynoeceum of Apocynaceae, traces to the perianth and stamens omitted save in figs. 53-57. Explanation in the text. Figs. 53-57, *Apocynum cannabinum*; figs. 58-61, *Stemmadenia Alfari*; figs. 62-65, *Cerebera Tanghin*; figs. 66-70, *Lacmellia edulis*; figs. 71-72, *Allamanda cathartica*. In these diagrams glandular tissue pertaining to the nectaries is stippled.





*Macrosiphonia Brachysiphon* (Torr.) Gray  
*M. Macrosiphon* (Torr.) Heller  
*Mandevilla Bridgesii* (Muell.-Arg.) Woods.  
*M. hirsuta* (A. Rich.) K. Sch.  
*M. illustris* (Vell.) Woods.  
*M. splendens* (Hook.) Woods.  
*Mascarenhasia elastica* K. Sch.  
*Mesechites trifida* (Jacq.) Muell.-Arg.

Essentially the same vascular organization is found in numerous other species and genera, which differ chiefly in that the residual stele consists of separate bundles, rather than a siphonostele:

*Allamanda cathartica* L.  
*Forsteronia viridescens* Blake  
*Lacmellia edulis* Karst.  
*Malouetia guatemalensis* (Muell.-Arg.) Standl.  
*Odontadenia Hoffmannseggiana* (Steud.) Woods.  
*O. Schippii* Woods.  
*Plumeriopsis Ahouai* (L.) Rusby & Woods.  
*Prestonia acutifolia* (Benth.) K. Sch.  
*P. portobellensis* (Beurl.) Woods.  
*Rauwolfia tetraphylla* L.  
*Rhabdadenia biflora* (Jacq.) Muell.-Arg.  
*Thenardia Galeottiana* Baill.  
*Thevetia peruviana* (Pers.) K. Sch.  
*Trachelospermum difforme* (Walt.) Gray  
*T. jasminoides* (Lindl.) Lem.  
*Urechites Andrieuxii* Muell.-Arg.  
*Zschokkea panamensis* Woods.  
*Z. ramosissima* Muell.-Arg.

In certain of the foregoing, repeated radial and tangential branching of the nectary bundles produces an elaborate "polydesmic" condition; in certain also the centripetal migration of the four placental bundles may occur before the branching outward of the nectary traces. In some, the four placental laterals may fuse into pairs composed of the adjacent laterals of either carpel, later dividing again before the complete organization of the ovary (cf. figs. 67-69 inclusive). But such variations may be encountered occasionally within flowers of a single species, and thus appear relatively insignificant.

#### *Stemmadenia*

The most elaborate and confusing system of vascular supply for the gynoeceium is found in the investigated species of *Stemmadenia* and certain



more or less closely related genera. In *S. Alfari* (cf. figs. 58-61 inclusive), the departure of the corolline and staminal bundles leaves an elaborately dissected residual stele composed of many bundles uniseriately arranged in roughly circular outline (fig. 58). These commence an extended system of branching, both radially and tangentially, until the stele consists of innumerable strands occupying the receptacle in a manner almost "monocotyledonous" (fig. 59).

At no time are the midribs and placental laterals distinguishable as such. Nevertheless a definitely glandular development of the outermost tissue strongly suggests the adnation of an annular nectary to which the outermost vascular bundles probably are referable.

The scattered bundles merely crowd away to allow the formation of the carpellary cavities; after which those which are to supply the carpels are definable by forming an invaginated arc about the two cavities. The bundles other than this single series proceed up into the nectaries, which remain adnate to the ovary save very shortly at the upper margins (figs. 60, 61). "Polydesmy" therefore frequently is characteristic of the nectaries, and never of the carpels proper.

Other species having a gynoeceal anatomy similar in general to that of *S. Alfari* include:

- Funtumia elastica* (Preuss.) Stapf
- Stemmadenia grandiflora* (Jacq.) Miers
- S. obovata* (Hook. & Arn.) K. Sch.
- Tabernaemontana acutissima* Muell.-Arg.
- T. arborea* Rose
- T. chrysocarpa* Blake
- T. Cumingiana* A.DC.
- T. divaricata* R.Br.

#### *Cerbera*

The vascular anatomy of apocynaceous ovaries which are unaccompanied by nectaries shows great uniformity. That of *Cerbera Tanghin* Hook. (figs. 62-65 inclusive) may illustrate this group. After the departure of the corolline and staminal traces the receptacular stele is seen to constitute a hollow cylinder consisting of several distinct bundles, or rarely a poorly organized siphonostele which soon becomes dissected (fig. 62). At this stage the midribs ordinarily are not obvious as such.

Soon, however, the number of bundles increases by tangential branching, and the stele thus increased undergoes a furrowing in two opposed positions to form the vascular supply of the respective carpels (figs. 63, 64), the cavities of which shortly make their appearance. By this time

the carpels are organized fully, and the midribs usually are somewhat larger than the lateral veins, but never is this difference very pronounced (fig. 65). As appears to be invariable in the Apocynaceae, the midribs proceed into the common style, the lateral traces disintegrating distally. Other genera and species which are destitute of gynoeceal nectaries and show an ovarian anatomy similar to that of *C. Tanghin* include:

*Adenium coetanium* Stapf  
*Amsonia ciliata* Walt.  
*Cycladenia humilis* Benth.  
*Haplophyton cimicidum* A.DC.  
*Nerium Oleander* L.  
*Pleiocarpa bicarpellata* Stapf  
*Plumeria rubra* L.  
*Rhazya orientalis* (Dcne.) A.DC.  
*Strophanthus dichotomus* A.DC.  
*S. gratus* A.DC.  
*S. sarmentosus* A.DC.

Although the foregoing appear superficially to be destitute of a nectary about the ovary, and no vascular tissue to supply such an organ exists, several genera (cf. *Cycladenia*) possess carpels which are united for a short distance at the very base, where a rather poorly defined glandular development of the superficial tissues occurs.

#### *Apocynum*

The vascular anatomy of the gynoeceium of *Apocynum* and *Trachomitum*, both members of the small subfamily *Apocynoideae*, differs so markedly from that of other members of the Apocynaceae, and is so closely involved with the vascular skeleton of the other components of the flower, that it appears necessary to present a condensed account of the anatomy of an entire, representative flower (cf. figs. 53-57 inclusive).

The stele of *Apocynum cannabinum* is rather irregularly 10-lobed in the lower receptacle (fig. 53). Of the ten, alternate lobes depart to provide the midribs of the five calyx and corolla members, and from each the respective laterals are produced according to the Type III calyx plan. As the perianth midribs depart they leave in their wake a rather indefinite number of small, poorly defined bundles to constitute the residual stele. Two opposed pairs of these bundles migrate toward the center of the stele to form the placental bundles of the two carpels in a manner similar to that observed for *Pleiocarpa*, *Cerbera*, and other genera. The residual stele remaining after the departure of the perianth traces, therefore, is devoted solely to the vascular supply of the two carpels.

Subsequent to their departure from the receptacular stele, however, it is found that the ten "perianth traces" are really compound structures. For the five staminal traces prove to be adnate to the calycine midribs; and, furthermore, *the corolline midribs are found to be adnate to the five bundles which supply the five gynoecial nectaries* (figs. 54-57) inclusive. The five nectary midribs, upon becoming free from the corolline midribs, branch tangentially to produce a somewhat variable number (usually two) of laterals. Full tissue differentiation of the calyx, corolla (with the epipetalous staminal filaments), nectaries, and carpels is obtained at about this time.

This curious adnation of the staminal to the calycine traces, and of the nectary to the corolla traces, has been observed only amongst the following genera and species, all of which are referable to the subfamily Apocynoideae:

*Apocynum androsaemifolium* L.

*A. cannabinum* L.

*Trachomitum venetum* (L.) Woods.

The most striking and significant feature of this type of gynoecial skeleton is found in the fact that the carpellary and nectary vascular supplies are quite independent, removing as well the possibility of interpreting the nectaries as merely "enlargements of the receptacle or torus," and of no evolutionary significance.

#### EVOLUTIONARY MODIFICATION OF THE GYNOCIDIUM

We have observed that in *Pleiocarpa mutica* there can be found in a single cymule an almost perfect transition from four fertile carpels to two fertile carpels and two alternate, solid carpellodes. It has also been pointed out that the two nectaries which alternate with the fertile carpels of *Lochnera* and *Vinca* differ from the solid carpellodes of *Pleiocarpa* only in the fact that they do not contribute to the style. The "nectaries" certainly appear to be equivalent to the "carpellodes" both from the observed variation in *Pleiocarpa* and from the standpoint of comparative vascular anatomy. If the interpretation of the gynoecial nectaries as carpellodes be accepted, phylogenetic significance will be given to the diversity of modification amongst the nectaries, and to their various relationships to the ovary proper. A few Apocynaceae are polycarpellary at the present day; but the frequency of nectaries amongst the family as a whole would indicate polycarpy to have been the original condition probably throughout, or essentially so.

In many Apocynaceae the nectaries are completely free from the

ovary. But in others they are found to be adnate to the very base of the ovary. In certain genera and species the nectaries are adnate throughout their entire length, or free merely at their upper margins (cf. *Stemmadenia*, figs. 60, 61). When the adnation of an annular nectary is virtually complete, its presence may be determined superficially only by the somewhat enlarged, glandular base of the ovary (cf. pl. 5, fig. 4). When seen in transverse section, however, two more or less distinct vascular systems frequently are found, the outer pertaining to the adnate nectary, and the innermost to the carpels (cf. pl. 5, figs. 1, 2). That the cohesion and subsequent adnation of the cycle of nectaries may influence syncarpy of the ovary is indicated by the fact that in most syncarpous ovaries the presence of an adnate nectary cycle may be demonstrated, either by a glandular base of the ovary wall, or that together with a double vascular supply.

In some cases, as in *Cycladenia humilis*, the ovary may be syncarpous and bilocular for the basal half roughly, and apocarpous above. In such ovaries, although a second vascular system cannot be demonstrated, the syncarpous base is conspicuously glandular; and one easily assumes that although the nectary vascular supply has been eliminated the effects of adnation remain in the syncarpy and the glandular epidermis of the ovary base. It should be observed that this interpretation receives support from the fact that obviously simple, apocarpous ovaries of Apocynaceae never are provided with a glandular epidermis.

The peculiar adnation of the nectaries to the ovary of certain Apocynaceae recalls the current theory of "carpel polymorphism" (Saunders, 1925). And surely it appears that that theory should rest upon some such foundation as that found in Apocynaceae. But the observations which we have made necessitate no specious assumptions of "valve" and "solid" carpels, either "sterile" or "fertile," in confusing variety, the fallacy of which has been revealed so satisfactorily by Eames (1931). We wish to emphasize that our conception of the carpel is that of Eames and not of Saunders (1925). This may be effected most expeditiously, perhaps, by adding that Miss Saunders has expressed privately to the senior author that it is her conviction that the ovary of *Apocynum* consists of at least six carpels; two "sterile valves" plus four "fertile, solid carpels"; and that the nectaries are merely enlargements of the receptacle and of no particular significance.

#### DISCUSSION AND SUMMARY

Perhaps the chief interest in the floral morphology and anatomy of Apocynaceae is found in the interpretation of three categories of structure which are presumed to be vestigial:



(1). *The calycine squamellae* are small internal appendages at the base of the calyx lobes which are sufficiently constant in position, shape and number to form the basis of taxonomic differentiation of genera and species. These appendages usually are glandular and without vascular tissue. In a few genera, however, they are provided with small traces produced from the lateral veins of the calyx lobes. Therefore they are interpreted as stipular vestiges. Similar calycine appendages are found in certain other families of Gamopetalae. In one genus of Asclepiadaceae they have been construed as stipular in nature (Woodson, 1936) and future studies may lead to a similar interpretation in such families as Gentianaceae, Oleaceae, etc.

(2). *The corolline scales* likewise are internal appendages of the corolla which are of considerable taxonomic value. Where they are well developed these scales are found to have an interesting vascular anatomy, with the traces supplied as branches from the corolla lateral veins in a manner very similar to that found in many vegetative stipules such as those of *Pelargonium*. The corolline scales therefore also are interpreted as stipules. Various "coronas" and "scales" are found upon the petals of many flowering plants, such as Caryophyllaceae, Gentianaceae, Asclepiadaceae, etc. Subsequent investigations may well reveal these, also, as stipular vestiges and the corolline members as essentially foliar in nature.

(3). *The gynoeceal nectaries* constitute a cycle of two to five more or less fleshy, ovoid bodies about the base of the ovary. Occasionally the nectaries cohere to form an annular structure. Previous studies by the senior author (Woodson, 1930) had shown the vascular organization of these structures to be rather similar to that of the fertile carpels. In the present investigations an almost perfect transition from four fertile carpels to two fertile carpels and two alternate solid carpellobes has been demonstrated to occur in a single cymule of *Pleiocarpha mutica*. The nectaries of other Apocynaceae, such as *Vinca* and *Lochnera*, differ from the carpellobes of *Pleiocarpha* essentially only in the fact that they do not contribute to the style. Hence the interpretation of the nectaries as carpellobes finds additional support.

In some genera a peculiar condition is found in which the nectaries cohere mutually and become adnate to the functional ovary, giving rise to a phenomenon which the writers wish to emphasize as not coinciding with the theory of "carpel polymorphism." Apocynaceous ovaries of several genera which appear to be simple from ordinary dissections are found to bear rather obscure traces of such nectarian adnation.

The interpretation of the nectaries as constituting a cycle of carpellobes apparently would indicate the derivation of Apocynaceae from poly-

carpellary ancestors; and the presence of stipular vestiges in the calyx and corolla, as well as at the vegetative node, might indicate a phylogenetic relationship with the extant order Rosales. Similar gynoeceal nectaries occur in other families of Angiospermae such as Caryophyllaceae, Primulaceae, Gentianaceae, Convolvulaceae, Solanaceae, Caprifoliaceae, etc. and probably would repay similar study. The hypogynous "disc" of *Mertensia* (Boraginaceae) recently has been interpreted as of carpelode origin by the junior author (Moore, 1936).

*The vascular anatomy of the calyx* is found to be of interest in that there is an apparent transition from the 3-trace unilocular to the 1-trace condition of the lobes. Although four general types of organization are encountered predominantly, an almost bewildering variation occurs, occasionally amongst flowers of a single inflorescence.

Although we believe that contributions of some value have been made to the phylogeny of Apocynaceae through our investigations, it must be granted that the results appear to be of little value to pure taxonomy. The vascular systems of the calyx, for example, do not coincide in general with existing classifications, and neither do they support the erection of a more satisfactory system. It probably should be assumed that the present systematic divisions of the family, which appear fairly natural upon their basis of gross morphology, are of great antiquity and have undergone parallel evolution of a certain degree.

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## Explanation of plates

(All photomicrographs from transverse sections unless otherwise stated)

## PLATE 3

Fig. 1. Pedicel of *Rawolfia tetraphylla* L., showing invasion of the pith by strands of internal phloem. ( $\times 45$ )

Fig. 2. Same as fig. 1, showing tracheid of protoxylem (*t*) differentiated within a medullary strand of internal phloem. ( $\times 230$ )

Fig. 3. Vegetative node of *Mandevilla Bridgesii* (Muell.-Arg.) Woods., showing origin of interpetiolar stipular appendages. ( $\times 16$ )

Fig. 4. Flower of *Mesechites trifida* (Jacq.) Muell.-Arg., general morphology: *ca*—calyx tube; *co*—corolla tube; *sq*—squamellae; *n*—nectaries; *o*—ovary. ( $\times 12$ )

Fig. 5. Vegetative node of *Prestonia acutifolia* (Benth.) K. Sch., showing origin of intrapetiolar stipular appendages. ( $\times 16$ )

Fig. 6. Flower of *Vinca minor* L., showing carpels and alternate nectaries. ( $\times 28$ )

Fig. 7. Sector of flower of *Mandevilla subsagittata* (R. & P.) Woods., longitudinal section, showing nectary (*n*) and squamella (*sq*). ( $\times 28$ )

## PLATE 4

Fig. 1. Sector of flower of *Mesechites trifida* (Jacq.) Muell.-Arg., showing marginal origin of squamellae (*sq*). ( $\times 50$ )

Fig. 2. Sector of flower of *Mandevilla Bridgesii* (Muell.-Arg.) Woods., showing squamellae (*sq*). ( $\times 50$ )

Figs. 3–4. Sector of flower of *Mandevilla subsagittata* (R. & P.) Woods., showing marginal origin of “opposite” squamellae. ( $\times 50$ )

Fig. 5. Sector of flower of *Funtumia elastica* (Preuss) Stapf, showing migration of squamella traces (*st*) from the calyx. ( $\times 50$ )

Fig. 6. Squamella of *Strophanthus gratus* A. DC. showing bicollateral trace (*st*) derived from calyx. ( $\times 210$ )

## PLATE 5

Fig. 1. Ovary of *Zschokkea panamensis* Woods. showing adnation of the annular nectary. The vascular systems of the nectary (*nt*) and the ovary proper (*ot*) remain distinct. The ovary is syncarpous but bilocular with axile placentation. ( $\times 17$ )

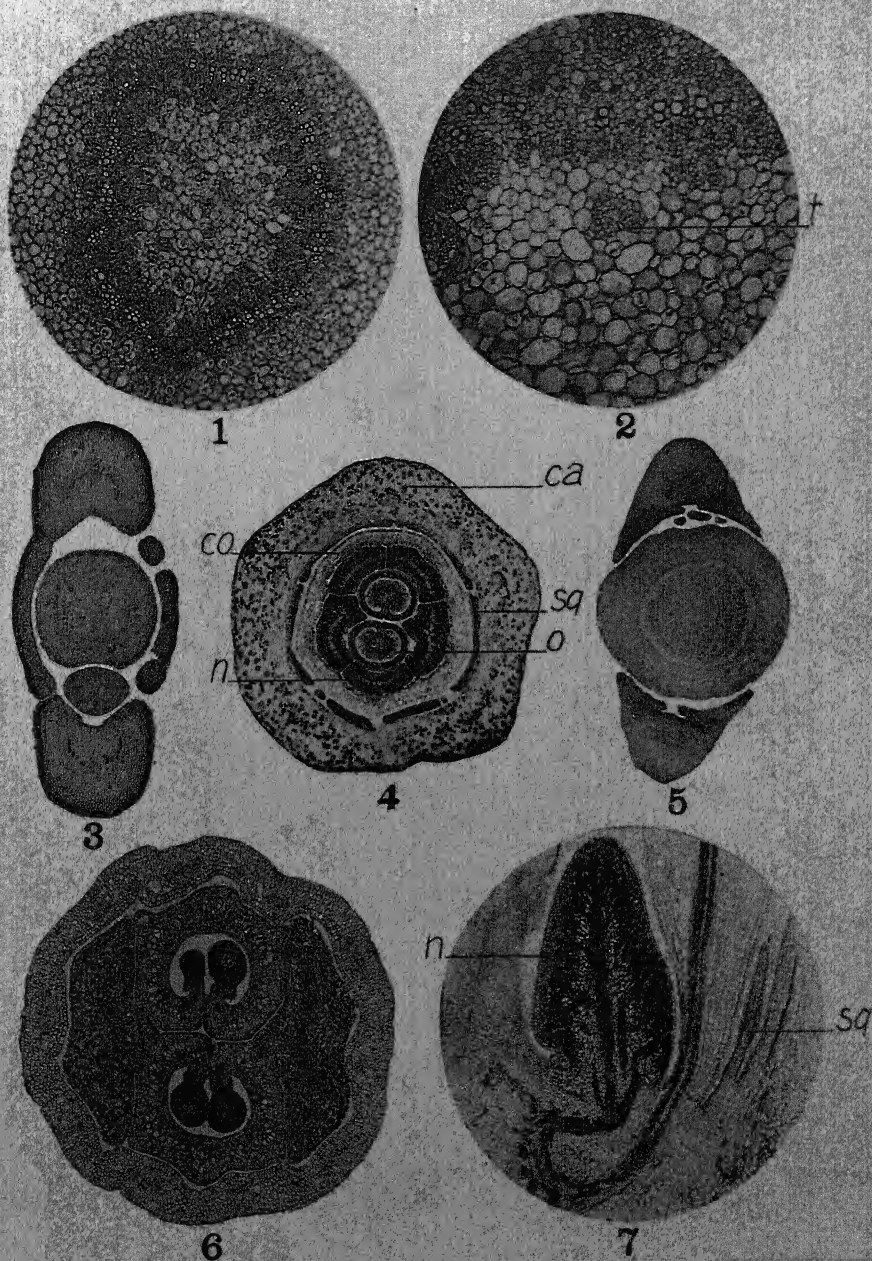
Fig. 2. Ovary of *Lacmellia edulis* Karst. showing adnation of the annular nectary. The vascular systems of the nectary (*nt*) and the ovary proper (*ot*) remain distinct. The ovary is syncarpous and unilocular with parietal placentation. ( $\times 17$ )

Fig. 3. Sector of flower of *Mandevilla subsagittata* (R. & P.) Woods., showing annular base of the nectaries which are free from the carpels which they surround. ( $\times 20$ )

Fig. 4. Sector of flower of *Tabernaemontana chrysocarpa* Blake, longitudinal section, showing adnation of the annular nectary (*n*). ( $\times 25$ )

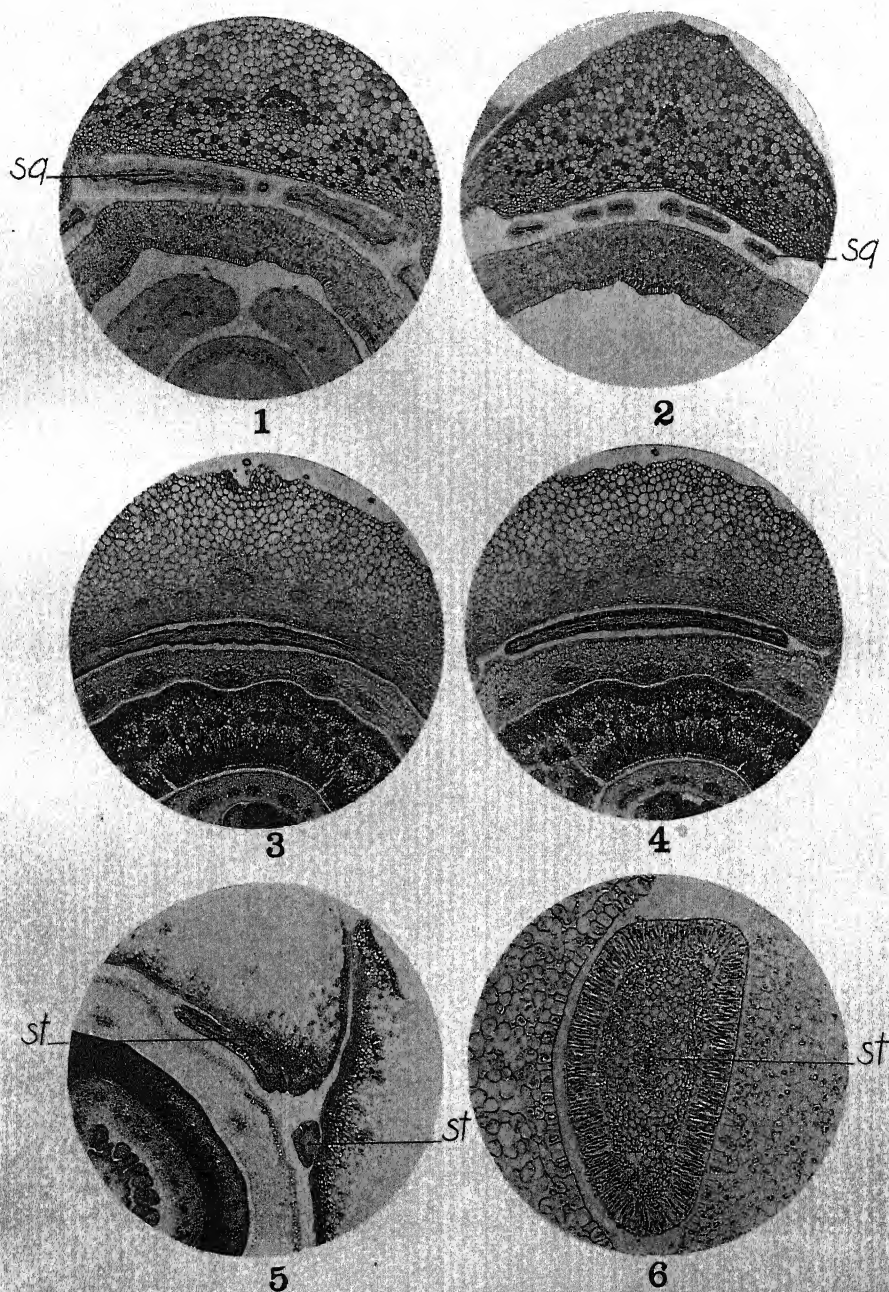
Fig. 5. Sector of flower of *Plumeria rubra* L., longitudinal section, showing the almost completely inferior ovary. ( $\times 25$ )

Fig. 6. Sector of flower of *Urechites Andrieuxii* Muell.-Arg., longitudinal section, general morphology: *ca*—calyx; *sq*—squamella; *co*—corolla; *a*—anther; *s*—stigma; *o*—ovary; *n*—nectary. ( $\times 25$ )



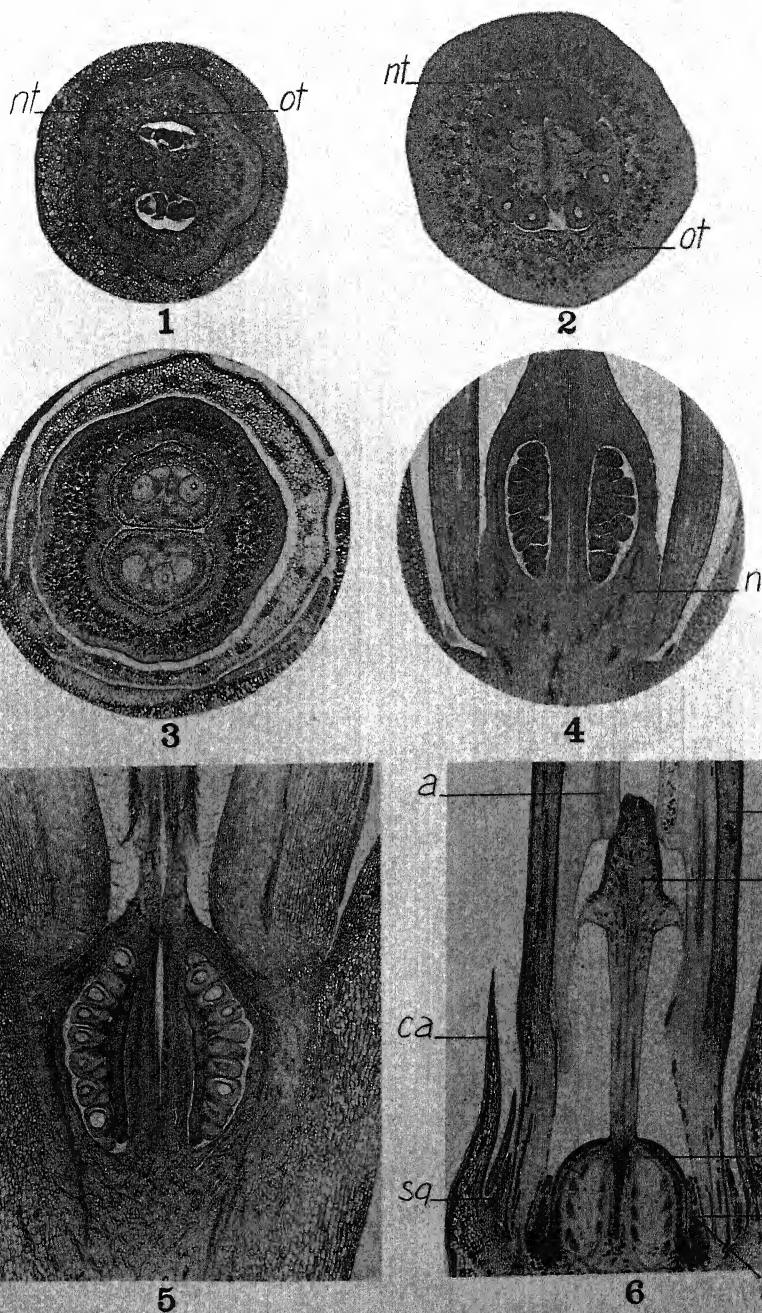














## Notes on fungi from the lower Mississippi Valley<sup>1</sup>

L. O. OVERHOLTS  
(WITH FIGURES 1-13)

From July until October of 1931 the writer was in the employ of the office of Forest Pathology of the United States Department of Agriculture. Most of this period was spent in a reconnaissance survey of timber decays and their causal fungi as they occur in the hardwood forests of the lower Mississippi Valley. Most of the time was spent in northeastern Louisiana in the region adjacent to the towns of Lake Providence and Ferriday, from which points excursions were made into adjacent Arkansas and Mississippi. About 500 collections of fungi, representing approximately 200 species, mainly of wood-inhabiting forms, were made and subsequently determined. These form the basis of the present report.

In the course of these investigations the writer was accompanied at times by members of the Forest Pathology division of the Southern Forest Experiment Station at New Orleans, and throughout the summer by Mr. Frank Kaufert without whose assistance the list would be much less complete. In the identifications I have had also considerable assistance from Mr. Ross W. Davidson of the Washington Office of Forest Pathology. Dr. C. L. Shear and Miss Edith K. Cash have made some identifications of collections falling into their special fields. Several collections of resupinate Hymenomycetes still remain to be determined, but it is impossible, because of the existing chaos in the genera to which they belong, to complete them at this time.

The generally dry atmospheric conditions which had prevailed during the preceding two years was both an advantage and a handicap; the former because it enabled us to penetrate swamp lands that normally are more inundated and inaccessible, and the latter because of its probable effect in reducing the number of species and collections obtained. This last item was in part overcome by the fact that during the summer of 1931 itself, rains, though not always heavy, were frequent enough during July and August to produce at least a fair crop of sporophores.

Viewed against a background of collecting in the wooded areas of the Allegheny Mountains the bottom hard-wood lands along the lower Mississippi River present some interesting contrasts. In the *Polyporaceae* there is the usual abundance of sap-wood inhabiting species, and the usual paucity of sporophores of heart-wood decaying species, or if sporo-

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phores of the latter group are slightly more abundant it may be due to the presence of certain species inclined to fruit more prolifically, and seldom found in the Allegheny region. But in other families the differences are more striking, if one may consider the summer of 1931 as approaching normality. One is particularly impressed by the lack of both individuals and species in the families Agaricaceae, Boletaceae, and Clavariaceae. While little attempt was made to collect specimens in these groups except for wood-inhabiting Agaricaceae, very few species were encountered. The Russulae and Lactariae that occur so abundantly in favorable seasons in the Allegheny region seem rare indeed, and terrestrial species of other genera were rarely seen. A single bolete, *Boletus chrysenteron* was common enough, but few others were seen. In the Clavariaceae not a single specimen was observed. Terrestrial Hydnaceae were likewise absent. In the Thelephoraceae, the wood-inhabiting species seemed fairly common, but here again terrestrial forms were rare.

In the Polyporaceae new information has been obtained on a considerable number of species. The status of *Polyporus ludovicianus*, a little known species, has been cleared up, and the species shown to be of great importance in causing an extensive butt-rot in *Quercus* and *Liquidambar*. It fruited abundantly and it is surprising that it has so long remained obscure. *P. fissilis* was collected in abundance and likewise proved to be highly important in the pathology of both *Quercus* and *Liquidambar*. An extensive and highly characteristic large pocket rot of *Quercus* is now rather definitely attributed to *P. zonalis* although some further study of that species is highly desirable in the light of the fact that essentially the same rot occurs in much more northward stations, apparently attributable to either or both *Poria undata* and *Polyporus rigidus*, all of which, however, have sporophores that are very similar in their essential characters. *P. sulphureus* seems to be just as ubiquitous in Louisiana as in more northern regions, while *P. dryophilus* and *P. dryadeus*, long known for their heart-rotting propensities in northern oaks, are strangely uncommon or occur not at all in this region. *P. lucidus* has been shown to be the cause of extensive heart decays in living *Quercus*, and this information came as a considerable surprise. *P. hispidus* is common on living *Quercus* and likewise causes an extensive and rather important decay, and as seems to be true in the north, is usually associated with the occurrence of conspicuous elongated wounds or cankers. *P. palustris* seems to cause an extensive brown heart-rot in living pine, and this relationship has not previously been reported. The same is true for *Fomes Calkinsii*, or its near relative *F. robustus*, on *Quercus*, but the species is probably not so

important. No additional information was secured as to the cause of "pecky cypress" but it is a safe assumption that it is not caused by *Fomes geotropus* as has been stated.

Owing to the fact that the relatively small amount of collecting that has previously been done in this region has not emphasized the pathological aspects of the situation, much new information has been secured as to generic substrates of numerous species of timber-inhabiting fungi. Most of this, together with additional notes, will be presented with each species.

Specimens of a considerable number of the species collected are deposited at the Southern Forest Experiment Station in New Orleans. A larger and nearly complete representation of species has been deposited in the office of Forest Pathology at Washington. A nearly complete representation of both species and collections is in the writer's herbarium, while certain duplicates have been filed in the herbarium of the Pennsylvania State College.

While considerable collecting was done in each of the states of Louisiana, Mississippi, and Arkansas, the species listed are to be regarded as originating in Louisiana unless otherwise specified by state abbreviations.

#### ASCOMYCETES

*Bolinia tubulina* (A. & S.) Sacc. on *Gleditsia*. *Cenangella Ravenelii* (Berk.) Shear on *Ilex*. *Daldinia concentrica* (Bolt.) Ces. & deNot. on *Diospyros*. *Dothichloe atramentosa* (Berk. & Curt.) Atk. on *Sporobolus Berteroanus*. *Hypocrea rufa* (Pers.) Fr. on *Quercus*; *H. sulphurea* (Schw.) Sacc. on *Liquidambar*. *Hypoxylon atropunctatum* (Schw.) Cooke on *Fagus*; *H. botrys* Ell. & Ev.; *H. haematostromum* Mont.? on *Fraxinus*; *H. rubiginosum* (Pers.) Fr. *Lachnum virgineum* (Batsch) Karst.? on *Taxodium*. *Nectria sanguinea* (Bolt.) Fr. on *Liquidambar*. *Nummularia clypeus* (Schw.) Cooke. *Phyllachora graminis* (Pers.) Fuckel on *Panicum*. *Rhytisma acerinum* (Pers.) Fr. on *Acer rubrum*; *R. Vaccinii* (Schw.) Aut. Am. on *Vaccinium arboreum* (La., Miss.). *Taphrina caerulescens* (Mont. & Desm.) Tul. on *Quercus nigra*.

#### FUNGI IMPERFECTI

*Cercospora rhoina* Cooke & Ellis on *Rhus* (Miss.). *Darlucula filum* (Biv.) Cast. on *Melampsora Medusae* on *Populus deltoides* (La.) and on *Uromyces Lespedezae-procumbentis* on *Lespedeza repens* (Miss.). *Dendrochium compressum* Ell. & Ev. *Dendrostilbella* sp. on *Celtis*. *Endothiella gyrosa* Sacc. on *Quercus*. *Phyllosticta acericola* Ell. & Ev. on *Acer rubrum*; *P. Labruscae* Thuem. on *Vitis*. *Septoria Rubi* var. *pallida* Ell. & Holw. on *Rubus*.

## BASIDIOMYCETES

## ORDER I. USTILAGINALES

*Entyloma australe* Speg. on *Physalis*. (Ark.)

## ORDER II. UREDINALES

*Coleosporium Solidaginis* (Schw.) Thuem. on *Solidago*; *C. Vernoniae* Berk. & Curt. on *Vernonia*. *Gymnosporangium germinale* (Schw.) Kern on *Pyrus* (Miss.). *Melampsora Humboldtiana* Speg. on *Salix*; *M. Medusae* Thuem. on *Populus deltoides*. *Phakopsora Crotonis* (Burr.) Arth. on *Croton capitatum*. *Puccinia Hydrocotyles* (Link) Cooke on *Hydrocotyle*; *Puccinia Polygoni-amphibii* Pers. on *Polygonum*; *P. Smilacis* Schw. on *Smilax*; *P. Xanthii* on *Xanthium* (Miss.). *Uromyces Lespedezae-procumbentis* (Schw.) Curt. on *Lespedeza repens* (Miss.); *U. Toxicodendri* Berk. & Rav. on *Rhus Toxicodendron*.

## ORDER III. HYMENOMYCETALES

## FAMILY AURICULARIACEAE

*Auricularia Auricula-Judae* (Fr.) Schroet. on *Celtis*, *Gleditsia*, *Liquidambar* and *Quercus*; common, with some specimens as much as 25 cm. broad (La., Ark.); *A. rosea* Burt. *Septobasidium pseudopedicellatum* Burt on *Crataegus*; *S. retiforme* (Berk. & Curt.) Pat. on *Quercus*.

## FAMILY TREMELLACEAE

*Eichleriella Leveilliana* (Berk. & Curt.) Mont. on *Crataegus*. *Exidia alba* (Lloyd) Burt. *Sebacina incrustans* (Pers.) Tul. on dead *Vitis* and at bases of living *Cornus* and other shrubs. *Tremellodendron pallidum* (Schw.) Burt.

## FAMILY DACROMYCETACEAE

*Calocera cornea* (Batsch) Fries on *Gleditsia*. *Ceracea corticioides* Ellis on *Taxodium*. *Guepinia spathularia* (Schw.) Fr. on *Liquidambar* and *Taxodium*.

## FAMILY THELEPHORACEAE

*Aleurodiscus acerinus* (Pers.) Hoeh. & Lit. on *Quercus*. *Asterostroma cervicolor* (Berk. & Curt.) Massee on *Planera*, *Quercus*, and other hardwoods. *Coniophora olivascens* (Berk. & Curt.) Massee on *Populus deltoides*. *Corticium chrysocreas* (= *Odontia Archeri*); *C. galactinum* (Fr.) Burt on *Pinus taeda*; *C. lactescens* Burt? on *Celtis*; *C. lividum* Pers. on *Quercus* (La., Ark.); *C. portentosum* Berk. & Curt. on *Gleditsia*; *C. stramineum* Bres. *Hymenochaete Curtisii* (Berk.) Morg. on *Quercus marylandica*; *H. epichlora* (Berk. & Curt.) Cooke. *Peniophora carnea* (Berk. & Curt.) Cooke on *Celtis*;



*P. cremea* Bres. on *Crataegus*; *P. gigantea* (Fr.) Massee on *Pinus*; *P. Roumeguerii* Bres. on *Acer rubrum*, *Carya*, *Crataegus*, *Diospyros*, *Quercus* (La., Ark.). *Stereum fasciatum* Schw. on *Quercus* (La., Miss.); *S. frustulosum* Pers. on *Quercus*; *S. fuscum* (Schr.) Quel. on *Acer*, *Celtis*, *Fraxinus* *Quercus*, and *Ulmus* (La., Ark.); *S. gausapatum* Fr. on *Quercus* (Ark.); *S. pargamentum* Berk. & Curt. (Fig. 4); *S. rameale* (Schw.) Fr. on *Cephalanthus*, *Quercus* (La., Ark.); *S. Ravenelii* Berk. & Curt.; *S. subpileatum* Berk. & Curt. on *Liquidambar* and *Quercus* (La., Ark.); *S. umbrinum* Berk. & Curt.

#### FAMILY HYDNACEAE

*Hydnum ochraceum* (Pers.) Fr. on *Liquidambar*, *Nyssa*, *Quercus* (La., Miss.); *H. pulcherrimum* Berk. & Curt. on *Liquidambar* and *Quercus* (La., Ark.). *Irpex cinnamomeus* on *Quercus*; *I. mollis* Berk. & Curt. on *Liquidambar*, *I. Ravenelii* Berk. on *Quercus*. *Odontia barba-Jovis* Fries; *O. brunnescens* n. sp. on *Liquidambar*; *O. ciliolata* (B. & C.) Miller; *O. farinacea* (Pers.) Bres; *O. fimbriata* (Pers.) Fr.; *O. macrodon* (Pers.) Bourd. & Galz.; *O. setigera* (Fr.) Miller on *Liquidambar*, *Planera*, *Ulmus*. *Radulum vinosum* n. sp.

Of the above species the following are worthy of further comment:

*Hydnum pulcherrimum* was one of the commonest fungi encountered. It is a sessile, white, soft species growing on logs and stumps or on wounded areas of living trees and specimens up to 15 cm. broad. Fresh specimens have a milky juice that becomes very sticky as it dries (fig. 2).

*Odontia brunnescens* n. sp. Resupinate, effused, membranous or subce-  
raceous, with a thin pruinose-agglutinated margin of pale cream color; hymenium not cracked, cream-buff to clay color or pale cinnamon (Ridgway) when dry, thickly set with dome-shaped or slightly elongate protuberances that are separate or slightly confluent, projecting 80–250 $\mu$  above the surface, broad and obtuse, barely visible to the unaided eye; in section with a slightly yellowish subiculum 60–80 $\mu$  thick, composed of a narrow and scarcely discernible substratal layer of horizontal hyphae from which arises a broader and very compact central region of sub-erect hyphae with a narrow incrustated layer along its lower edge and sometimes with some incrustation above, bearing the basidial layer; cystidia of two types, one projecting on the granules and between them, with sub-bulbous base and tapering and sharp-pointed apex, 4–6  $\mu$  diameter below and there rarely slightly incrustated, the other especially abundant in the granules, imbedded or reaching the level of the basidial layer, never conspicuous, incrustated, hyaline, 35–40 $\times$ 9–10 $\mu$ ; spore short-cylindric, smooth, hyaline, 4–6 $\times$ 2–3 $\mu$ .

On dead branch of *Liquidambar*. Type collected at Oak Grove, La., Aug. 17, 1931. (U.S.F.P. Herb. 50225; Overholts Herb. 15252) (figs. 1, 3).

The granules on the hymenial surface are broader than in most species of *Odontia*, but the presence of cystidia precludes reference of the plant to the genus *Grandimia*.

*Odontia fimbriata* (Pers.) Fries. On dead wood. Wildsville, La.

*Radulum vinosum* n. sp. Resupinate, effused for several centimeters, thin and adnate, without definite margin; hymenium with rather blunt teeth that are isolated or closely associated, up to 1 mm. long and 150–300 $\mu$  diameter, everywhere vinaceous-drab or fawn color on drying; in section showing a distinct subiculum 200–300 $\mu$  thick, composed of somewhat gelatinized and very densely arranged hyphae throughout, those toward the substratum sub-horizontal and those toward the hymenium sub-erect, no incrustation, apparently about 3–4 $\mu$  diameter and without cross-walls or clamps though too strongly gelatinized and agglutinated to be certain; basidia 2–3 $\mu$  diameter; spores allantoid, bacilliform, smooth, hyaline, 3–4 $\times$ 1 $\mu$ ; cystidia and gloeocystidia absent; crystals about 20 $\mu$  diameter scattered through the subiculum and in the teeth.

On dead wood of deciduous trees. Type collected at Ferriday. La., Aug. 1, 1931. (U.S.F.P. Herb. 55624; Overholts Herb. 15254).

The gelatinized hyphae of the subiculum and their arrangement and compactness suggests rather the genus *Phlebia*, but the teeth are too well developed and too isolated to permit reference there. It is unfortunate that color records of the fresh plants were not obtained in the field, but the color on drying is distinctive.

#### FAMILY AGARICACEAE

*Agaricus abruptibulbus* Peck. *Cantharellus cibarius* Fr. *Clitocybe decora* Fr. on Taxodium. *Flammula eccentrica* Peck. *Hypholoma incertum* Peck. *Lactarius lactifluus* (L.) Fr. (La., Ark.); *L. subvellereus* Peck. *Lentinus tigrinus* (Bull.) Fr. *Lepiota Morgani* Peck; *L. procera* (Scop.) Fr. *Marasmius iocephalus* (Berk. & Curt.) Penn.; *M. siccus* (Batsch) Fr. *Omphalia campanella* (Batsch) Fr. *Panus angustatus* Berk. on Carya; *P. laevis* Berk. & Curt. on Liquidambar; *P. rudis* Fr. on Pinus and Quercus (La., Miss., Ark.); *P. stypticus* (Bull.) Fr. on Quercus. *Pleurotus corticatus* Fr. on Carya (Ark.); *P. ostreatus* (Jacq.) Fr. *Schizophyllum commune* Fr. on Carya, Diospyros, Gleditsia, Liquidambar (La., Ark.). *Volvaria bombycina* (Pers.) Fr. on *Acer rubrum* and Liquidambar.

Of the above species none were particularly abundant. *Lentinus tigrinus* was not collected but several wood rot isolations yielded cultures that produced typical sporophores of that species. *Lepiota Morgani* was fairly common in grassy woods and especially along grassy roadsides. *Marasmius iocephalus* was collected several times and is easily recognized

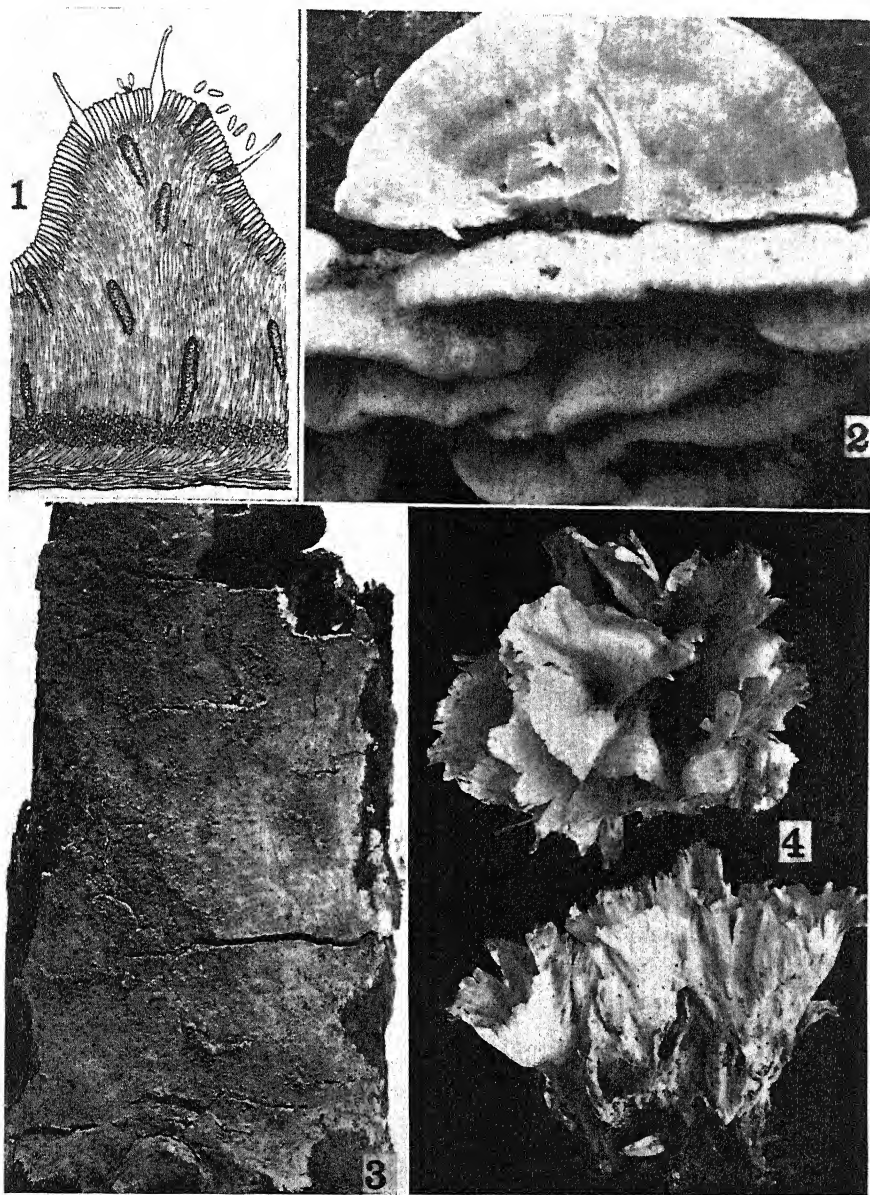


Fig. 1. Camera lucida drawing of section through a sporophore of *Odontia brunnescens*. Type collection.  $\times 600$ .

Fig. 2. Photo of *Hydnum pulcherrimum*. Upper specimen showing hymenial surface.  $\times \frac{1}{2}$ .

Fig. 3. Photo of type material of *Odontia brunnescens*.  $\times 2$ .

Fig. 4. Photo of fresh specimens of *Stereum pargamentum*.  $\times 1$ .

by its violaceous color. *Panus laevis* was found several times growing from wounded areas in living trees of Liquidambar. It is likely to be mistaken for a *Pleurotus* but the pileus and stem are both very hairy and the sporophore assumes a uniform yellow color on drying. *Volvaria bombycina* was found several times growing from knots in living trees.

## FAMILY BOLETACEAE

*Boletus chrysenteron* (Bull.) Fr. *Strobilomyces strobilaceus* Berk.

## FAMILY POLYPORACEAE

*Daedalea ambigua* Berk. on *Carya*, *Celtis*, *Diospyros*, *Gleditsia*, *Quercus* (La., Miss., Ark.); *D. confragosa* (Bolt.) Fr. on Liquidambar and *Quercus*; *D. elegans* (Spreng.) Fr. on *Carya* and *Gleditsia*; *D. farinacea* (Fr.) comb. nov. (*Irpex farinaceus* Fr.) on *Quercus*; *D. unicolor* (Bull.) Fr. on *Celtis*. *Fomes applanatus* (Pers.) Gill. on *Populus deltoides*; *F. Calkinsii* (Murr.) Sacc. & Sacc. on *Quercus*; *F. conchatus* (Pers.) Gill. on *Fraxinus*; *F. densus* Lloyd on *Carya* and *Fraxinus*; *F. fraxineus* on *Fraxinus*; *F. geotropus* Cooke on *Acer*, Liquidambar, *Magnolia*, *Populus*, *Ulmus* (La., Miss.); *F. igniarius* var. *laevigatus* (Fr.) Overh. (*Poria laevigata* Fr.) on *Fagus*, *Gleditsia*, *Quercus*; *F. lobatus* (Schw.) Cooke on *Quercus* (La., Miss.); *F. marmoratus* (Berk. & Curt.) Cooke on *Carya*, *Celtis*, *Diospyros*, *Gleditsia*, Liquidambar, *Quercus*, *Ulmus*; *F. Meliae* (Underw.) Murr. on *Fraxinus*, *Gleditsia* (La., Ark.); *F. rimosus* Berk. on *Robinia*; *F. tenuis* Karst.; *F. torulosus* on *Fraxinus* (Ark.). *Lenzites betulina* (L.) Fr. on Liquidambar, *Quercus* (La., Ark.); *L. saepiaria* (Wulf.) Fr. on *Pinus* (La. Miss., Ark.). *Polyporus abietinus* (Dicks.) Fr. on pine slash (La., Miss.); *P. adustus* (Willd.) Fr. on *Celtis*, *Gleditsia*, Liquidambar, *Quercus* (La., Miss., Ark.); *P. anceps* Peck on *Pinus taeda* (Miss.); *P. arcularius* (Batsch) Fr. on *Gleditsia*; *P. biformis* (Kl.) Berk. on *Carya* and *Quercus* (La., Ark.); *P. cinnabarinus* (Jacq.) Fr. on *Quercus* (La., Ark.); *P. cristatus* (Pers.) Fr. (Ark.); *P. Curtisii* Berk. on *Carya*, *Gleditsia*, *Quercus* (La., Miss., Ark.); *P. cuticularis* (Bull.) Fr. on *Acer*, *Celtis*, *Quercus*, *Ulmus* (La., Ark.); *P. dichrous* Fr. on *Carya*, *Cephalanthus*, *Fraxinus*, *Quercus*, *Ulmus* (La., Ark.); *P. distortus* (Schw.) Fr. on *Carya*, *Quercus* (La., Ark.); *P. dryophilus* Berk. on *Quercus*; *P. fimbriatus* Fr.; *P. fissilis* Berk. on Liquidambar and *Quercus*; *P. focicola* Berk. & Curt. (La., Miss.); *P. frondosus* (Dicks.) Fr. on *Quercus*; *P. galatinus* Berk. on Liquidambar and *Quercus*; *P. giganteus* on *Quercus*; *P. gilvus* (Schw.) Fr. on *Cephalanthus*, *Crataegus*, *Diospyros*, *Fagus*, Liquidambar, *Pinus*, *Quercus*, *Taxodium* (La., Miss., Ark.); *P. hirsutus* (Wulf.) Fr. on *Celtis*, *Nyssa*, *Populus*; *P. hispidus* on *Quercus* (La., Miss., Ark.); *P. hydroides* (Sw.) Fr. on *Carya*,



Gleditsia, Liquidambar, Ulmus; *P. lucidus* (Curt.) Fr. on Celtis, Diospyros, Liquidambar, Planera, Quercus (fig. 9); *P. ludovicianus* (Pat.) Sacc. & Trott. on Liquidambar and Quercus (La., Ark.); *P. maximus* (Mont.) Overh. on Ulmus; *P. mutabilis* Berk. & Curt. on Diospyros, Nyssa, Quercus (La., Ark.); *P. nidulans* Fr. on Carya; *P. obtusus* Berk. on Quercus; *P. palustris* Berk. & Curt. on Pinus (La., Miss.); *P. pargamenus* Fr. on Fagus and Liquidambar (La., Ark.); *P. persicinus* Berk. & Curt.; *P. pinsitus* Fr. on Fraxinus and Gleditsia (La., Ark.); *P. porrectus* (Murr.) Sacc. & Trott.; *P. radiatus* var. *Cephalanthi* n. var. on *Cephalanthus occidentalis*; *P. rhipidium* Berk. on Liquidambar and Quercus (La., Ark.); *P. robinophilus* (Murr.) Lloyd on Celtis (Miss.); *P. sanguineus* (L.) Fr. on Liquidambar and Quercus; *P. Schweinitzii* Fr. on Pinus; *P. sector* (Ehr.) Fr. on Carya, Liquidambar, Quercus (La., Ark.); *P. semipileatus* Peck; *P. Spraguei* Berk. & Curt. on Fraxinus, Liquidambar, Quercus (La., Ark.); *P. subectypus* (Murr.) Lloyd on Liquidambar; *P. submurinus* on Populus, Fraxinus, Quercus; *P. sulphureus* var. *cinnamatus* Morg. on Quercus; *P. supinus* (Sw.) Fr. on Carya, Diospyros, Fraxinus, Gleditsia, Liquidambar, Quercus, Ulmus; *P. tenuis* (Sacc.) comb. nov. (*Polystictus tenuis* Sacc.) on Taxodium; *P. versatilis* (Berk.) comb. nov. (*Trametes versatilis* Berk.) on Taxodium; *P. versicolor* (L.) Fr. on Liquidambar; *P. vinosus* Berk. on Liquidambar; *P. zonalis* Berk. on Carya, Celtis, Liquidambar, Populus, Quercus (La., Ark.). *Poria albocincta* Cooke & Massee; *P. ambigua* Bres. on Celtis and Liquidambar; *P. candidissima* (Schw.) Cooke; *P. eupora* Karst. on Quercus; *P. ferruginosa* (Schr.) Fr. on Liquidambar; *P. flaccida* sp. nov. on Carya, Liquidambar, Taxodium; *P. inermis* Ell. & Ev. on Ilex; *P. Langloisiana* Murr. on Liquidambar; *P. Langloisii* Murr. on Fraxinus and Quercus (La., Ark.); *P. medulla-panis* (Pers.) Cooke; *P. nigrescens* Bres.; *P. punctata* Fr. on Carpinus and Fraxinus (La., Ark.); *P. undata* Pers. on Fraxinus; *P. versipora* Pers. on Ilex and Quercus (La., Ark.). *Solenia candida* Pers. on Taxodium. *Trametes cubensis* (Mont.) Sacc.; *T. malicola* Berk. & Curt.; *T. rigida* Berk. & Mont. on Fraxinus and Carya; *T. sepium* Berk.

The following species of Polyporaceae are deserving of further notice here:

*Polyporus fimbriatus* has not previously been reported from the North American mainland. Its relationships have been confused due to the fact that the hymenium develops very differently at different times, so that the species has been classed in both Thelephora and Hydnum, and previous southern collections have been referred as forms of the thin and variable *Polyporus tenuis* or its near relatives. It grows from buried rotted wood in large soft white tough imbricate clusters like *Stereum pargamentum*,

and in fact my photo of that species (fig. 4) represents it very well from the upper surface view. It occurred several times in late July and early August after abundant rains.

*Polyporus fissilis* Berk. Soft and watery, white throughout, cartilaginous within or forming mucilaginous or soapy masses in the crevices near the fruiting bodies, drying yellowish; context strongly zonate; pores medium-sized, the pore surface slightly lavender (figs. 5, 12, 13).

On living Liquidambar and on living Quercus, especially *Q. nigra* and *Q. Phellos*. Common in central and northern Louisiana and in adjacent Mississippi and Arkansas. Produces hollows in butts and lower trunks of living trees, preceded by a soft, ropy, general, cinnamon-colored or whitish decay of the heartwood, with persistent medullary rays. One of the most destructive heart-rotting fungi of the region, the decay either a butt rot or a trunk rot. Occasionally on logs down two or three years. Sporophores are frequently abortive, producing no tubes. The species is widely distributed in the eastern United States but northward it is very sporadic in appearance and has never been regarded as of any importance in Forest Pathology. Although observed many times in some stage of fruiting, no sporophores were seen that were not within reach from the ground, indicating that it is most frequently to be found as a butt-rot.

*Polyporus ludovicianus* (Pat.) Sacc. & Trott. This species has received little attention from mycologists. It was originally described from Louisiana. Lloyd considered it to be a form of *P. cuticularis*. Probably less than a dozen collections were known prior to 1931. We found it to be a rather common species and several collections were made. It grows in imbricate clusters after the manner of *P. sulphureus*, the clusters sometimes as much as 45 cm. broad. The entire sporophore is brown or rusty-ochraceous in color with thin applanate pilei, zoned and matted-tomentose on the upper surface. The spores are like those of *P. cuticularis*, brown in color, 5-6×

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Fig. 5. Photo of cut in log of *Liquidambar styraciflua* showing hollow and rot produced by *Polyporus fissilis*, and at right and left masses of white fungous material of soap-like consistency taken from inside log at this point. Cut made at 19 ft. above stump. Greatly reduced.

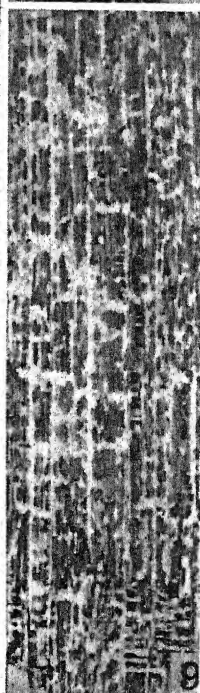
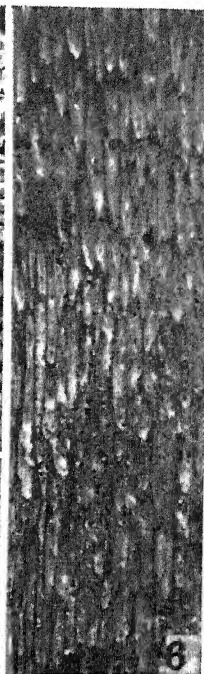
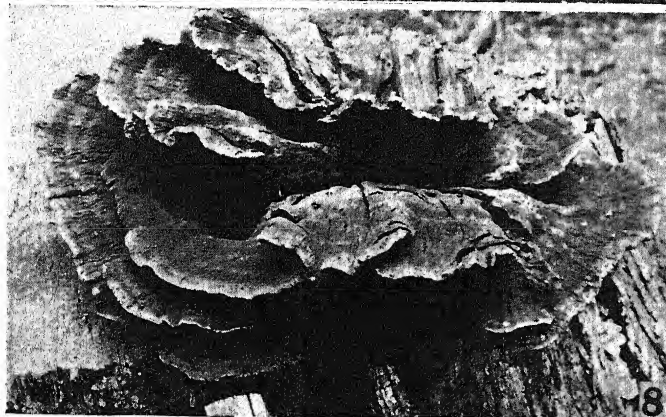
Fig. 6. Showing advanced stage of rot in Liquidambar, as seen in tangential section view, caused by *Polyporus ludovicianus*.  $\times 1$ .

Fig. 7. Heart rot in living Quercus, caused by *Polyporus sulphureus*. Greatly reduced.

Fig. 8. Imbricate sporophore mass of *Polyporus ludovicianus* growing on top of Quercus stump at Oak Grove, La.  $\times \frac{1}{4}$ .

Fig. 9. Photo of heart rot in living Quercus, caused by *Polyporus lucidus*.  $\times 1$ .





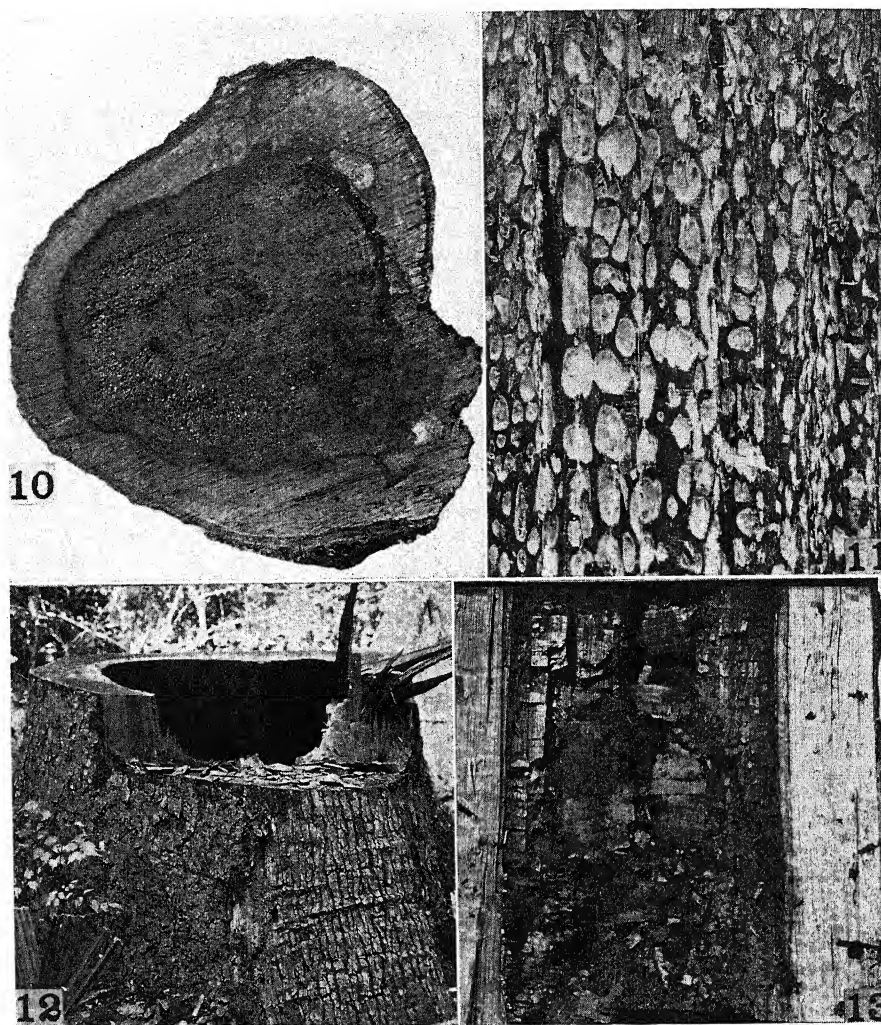


Fig. 10. Photo of cross section of log of *Quercus* with advanced stage of decay by *Polyporus hispidus*.  $\times \frac{1}{4}$ .

Fig. 11. Photo of large pocket rot in *Quercus*, probably produced by *Polyporus zonalis*.  $\times 1$ .

Fig. 12. Photo of stump of *Liquidambar* showing large hollow produced by *Polyporus fissilis*. This stump is of the same tree shown in Fig. 5. Greatly reduced.

Fig. 13. Advanced stage of rot of heartwood in *Quercus*, caused by *Polyporus fissilis*. The persistent medullary rays are characteristic of the rot on this host.  $\times \frac{1}{3}$ .

3.5–4  $\mu$ . Setae are not present and in this character it differs from the last-named species. It fruits only at the bases of living trees or quite as often on or about stumps of Liquidambar and Quercus. It produces a conspicuous speckled pocket-rot of the heartwood and seems to be one of the most destructive heart-rot organisms of the region. The pockets produced resemble those by *Stereum frustulosum* and *S. subpileatum*. The species proves to be rather widely distributed in the southern states, and collections are now known from South Carolina, Georgia, Alabama, Louisiana, and Texas (figs. 6, 8).

*Polyporus persicinus* Berk. & Curt. This species was originally described from South Carolina and has been collected but three or four times. Type fragments are said to be found at Kew and were studied by Murrill who reported that the description does not seem to apply to the type specimens and our present conception of the species is based on the type specimens rather than on the description. Coker twice collected the species at Chapel Hill, North Carolina, in this sense, and his specimens are at New York. I collected it once near Eudora, Ark. The species has considerable resemblance to the well developed centrally stipitate form of *P. distortus*. It grows on the ground though is probably attached to buried wood. The pilei are 10–25 cm. diameter, buffy-brown to pinkish brown when fresh but becoming sordid refescent-brown in age or on drying and the context of fresh specimens changes to a brownish-flesh-color where exposed, and is very friable and pale-brown on drying.

*Polyporus radiatus* var. *Cephalanthi* n. var. Sporophore practically resupinate, with only a tumid margin, yellowish-brown, tough; context brown; pore surface dark brown, the tubes 1–3 mm. long, their mouths averaging 4 to 5 per mm.; setae present, many with curved tips; spores nearly or quite hyaline, 4–4.5  $\times$  3.5–4  $\mu$ .

On dead standing *Cephalanthus occidentalis*. Common in northern and central Louisiana and at Eudora, Ark. Observed at many different stations. Never found with more than a suggestion of a pileus, which, together with the unusual and restricted habitat and the hooked setae almost make it worthy of specific recognition, especially since *P. radiatus* is not known to occur in its pileate form so far southward.

*Polyphorus sulphureus* var. *cinnatus* Morgan. Forming imbricate or rosette-like clusters 10–50 cm. broad, the pilei salmon-colored above, white below, fleshy at first, finally brittle; otherwise it resembles the species except that it always occurs at the bases or on the roots of living trees of Quercus, apparently from the ground, but in reality producing a pseudo-sclerotium, often of considerable length leading to infested roots. This

pseudo-sclerotium exudes milky drops where broken. The present form is described in more detail by Rosen (*Mycologia* 19: 191. 1927) August. Collected but once, at Oak Grove, La. Produces a carbonizing cubical rot of the heartwood (fig. 7). When heartwood heavily infested by the mycelium of this fungus is cut into, drops of a milky fluid collect on the cut surface of the wood.

*Poria flaccida* n. sp. Resupinate, annual, entirely white or drying cream-colored, soft and watery when fresh, drying rather soft; margin white, mycelioid and cobwebby over the adjacent bark; subiculum very thin and delicate, cottony, white; pore surface even, the tubes up to 1 mm. long, their mouths angular, thin-walled, entire, averaging 3 to 4 per mm.; spores almost exactly globose, smooth, hyaline,  $4-4.5 \times 4 \mu$ ; cystidia none; basidia  $4-5 \mu$  diameter; hyphae flexuous, simple or sparingly branched, thin-walled and flaccid, with frequent cross walls but no clamps, diameter  $2.4-3 \mu$  in trama,  $3-4 \mu$  in subiculum.

On old logs of *Carya*, *Liquidambar*, and *Taxodium*. Louisiana. Type collected near Kilbourne, La., Aug. 14, 1931, on *Carya* log (U.S.D.A. For. Path. Herb. 50356; Overholts Herb. 14073); also collected near Ferriday, La. This species is a close relative of *P. ambigua* Bres. but differs in the globose spores and the somewhat smaller hyphae.



## A genetic analysis of the inheritance of fragrance of gladiolus.

FORMAN T. McLEAN

This study was undertaken for the purpose of developing and intensifying fragrance in the gladiolus. Two of the ten or more fragrant species of the genus *Gladiolus*—i.e. the highly variable *G. tristis* and equally variable *G. recurvus*, were intercrossed and records were kept of their progeny in the first and second generations and in a back-cross, to learn the mechanism of inheritance of fragrance in them. In all 2,200 individuals were studied, comprising 194 crosses. Fairly complete descriptions were made of these, and this mass of data was tabulated under twenty-five characters, two of which are of fragrance; a night fragrance derived from *G. tristis* and a violet-like daytime fragrance from *G. recurvus*. The clones of the two species used were apparently homozygous for the characters for fragrance, but for many of the other characters they were evidently heterozygous. This was to be expected, since the wild forms of both species vary greatly in color and markings, but have characteristic fragrance, and leaf and sheath characters.

Through the liberal cooperation of the officers and personnel of the Works Progress Administration, whose assistance it is a pleasure to acknowledge, this material was tabulated and compared in detail. The statistics were handled by Mr. Erwin Jarmel, who did excellent work on it. Only one phase is treated here.

The results clearly indicate that the two primary types of fragrance are inherited differently. The lily-like night fragrance of *G. tristis* is apparently recessive to the absence of it, and dependent on two factors for its transmission, one of which must be homozygous for its expression, but the other heterozygous. The violet-like recurvus fragrance is dominant and appears to require two factors, both of which may be heterozygous. Recurvus fragrance is also epistatic to tristis fragrance in certain combinations. Of the twenty-three other characteristics recorded, only four have evident relationships to fragrance; two to tristis fragrance, one to recurvus, and one to both. Considering the heterozygosity of these other factors, no linkage groups can be postulated here to further substantiate or tend to disprove the two-factor hypothesis for the inheritance of each type of fragrance. But the evidence for it seems sufficient in itself.

Two new types of fragrance, each more pronounced than the primary species types, were found in the hybrids. Further studies of these to learn their manner of inheritance, and studies of the transmission of fragrance to crosses of these species hybrids with the garden varieties of gladiolus are in progress. Both show promise.

## REVIEW OF LITERATURE

There has been comparatively little breeding work to develop or intensify scent in flowers, and most of the workers have left no record of the inheritance of scent, except in very broad generalizations. Hampton<sup>1</sup> summarizes these observations. A preliminary report of the present work with gladioli was printed in 1933.<sup>2</sup> As already noted there, this was not the first attempt to produce fragrant gladioli. Dean Wm. Herbert reported the same cross in 1818 in a letter to the Royal Horticultural Society, London<sup>3</sup> and he subsequently named his hybrids *Gladiolus fragrans*. But that was long before the days of modern genetics, and there is no evidence that he carried the experiment beyond the first generation.

One reason for the lack of information on inheritance of fragrance is the inexactitude of the standards for odors and the mixed character of most of the natural ones, which are usually made up of several odors blended together. Hampton (loc. cit.) classifies odors of plants into ten groupings: (1) Indoloid or foetid, as in *Stapelia* and other carrion flowers; (2) Animoid or stale, as in hawthorn blossoms; (3) Heavy and sweet, as in jasmine; (4) Aromatic or sweet and spicy, as in clove carnation, night scented tobacco, etc.; (5) Violet or orris; (6) Rose; (7) Lemon, as in oranges and magnolias; (8) Fruit scented, as in *Philadelphus microphyllus*; (9) Animal and unpleasant, as in the lizard orchid; (10) Musk and honey, as in the musk plant and musk orchid.

Of these ten groupings, the fragrances dealt with here are:

- I—*Gladiolus tristis* scent, a night scent belonging to class (4) Aromatic, possibly combined with some of class (7) Lemon.
- II—The "Violet" scent of *Gladiolus recurvus* which is the strongest early in the morning and persists during the day, obviously belongs to class (5) Violet, possibly with other modifying elements in it.

Derived from these are:

- III—"Lemon" scent, a daytime scent found in some of the hybrids, and:
- IV—"Pungent," another daytime scent, occurring principally among the  $F_2$  and later crosses.

Each of these four scents is clearly distinguishable, both by its time of occurrence, day or night, and by its dominant odor component, but it is quite probable that each is not a simple odor, rather a combination of

<sup>1</sup> Hampton, F. A. "Flower scent," pp. 104-106. London, 1925.

<sup>2</sup> McLean, Forman T. "The inheritance of fragrance in *Gladiolus* species crosses," Jour. N. Y. Bot. Garden 34: 73-80. 1933.

<sup>3</sup> Herbert, Wm. "Instructions for the treatment of *Amaryllis longifolia* as a hardy aquatic, with some observations on the production of hybrid plants, etc." Trans. Hort. Soc. London, 3: 187-196. 1820.



two or more. For each plant recorded, the quality of the fragrance is set down according to the above groupings, and its intensity, whether faint, medium or strong. Observed differences in intensity are not treated in the present analysis; the personal element enters too strongly into the perception of scent, as recently proven by the studies of Blakeslee<sup>4</sup> All of the observations of fragrance here reported were made by the author, with the corroboration of two co-workers, Miss Helene Lunt and Mrs. Harry A. Jennison, whose perceptions of scent were about the same as his. If the work had been done by a number of people, differing in the keenness of their perceptions, such consistent results would not have been possible; a person with keener sense of smell might have detected scent where the author did not, as actually happened in the case of a gladiolus scent not discussed here. On the other hand, many visitors proved to be insensitive to one or the other of the odors treated in this paper. So the results reported may be regarded as simply one man's consistent observations.

#### RESULTS

This study was begun at the Rhode Island Agricultural Experiment Station in 1925, and continued at the New York Botanical Garden from 1928 to 1937. The Boyce Thompson Institute for Plant Research, through the kindness of Dr. Crocker, worked out for me the pregermination cold treatment necessary for the germination of the seeds of these small gladiolus species and hybrids, the chemical treatments to break the dormancy of gladiolus corms, and the effect of supplemental light on blooming time.

The results here reported were based principally on hybrids derived from one clon each of *Gladiolus tristis* and of *Gladiolus recurvus*. A second clon of *G. recurvus* was used for the production of some first generation hybrids, and these are treated separately for comparison.

The *G. tristis* used is designated Tristis II, and was obtained from C. G. Van Tubergen & Co. as *G. tristis concolor*. The flowers are clear greenish cream, large for the species, and only two to four on each spike. The general characteristics of this clon, which was used as the seed parent of all of the F<sub>1</sub> hybrids here treated, are given in detail in the discussion after table 1.

The *G. recurvus* clon used principally in this study is called *Recurvus Bronze*, and was obtained from A. J. Kruijff, of South Africa, who called it the best and strongest growing form of the species. In greenhouse culture

<sup>4</sup> Blakeslee, Albert F. "Demonstration of differences between people in the sense of smell," *Scientific Monthly* 41: 72-84. July, 1935.

here it is a weak grower, like all of *G. recurvus*, with rather flatter greyish leaves than the type, and light purplish bronze flowers instead of the typical violet or cream.

In series #55 of the first generation hybrids, a second clon of *G. recurvus* was used, called *Recurvus Violet Purple*. This was typical of the species.

In table 1, the distribution of the twenty-five recorded characteristics, including those for fragrance, are compared in the first generation hybrids, in series #55 (columns 2 and 3), in which *Recurvus Violet Purple* was the pollen parent; in series #60 (columns 4 and 5), in which *Recurvus Bronze* was used; in the second generation (columns 6 and 7), derived from series #60; and a back-cross in which  $F_1$  #60 was recrossed with *Tristis II*. In the discussion of the results as given in the table, the characteristics of the species clons used as parents are also taken up.

The columns headed "N" give the number of individuals in each category. Observations are incomplete for certain characters of a few individuals, so that the total records on many characters do not add up to the total number of individuals studied, but the number of such omissions is believed to be not great enough to seriously affect the percentage distributions.

TABLE 1

*Inheritance of twenty-five observed characters in first generation, second generation and back-cross of Gladiolus tristis and Gladiolus recurvus*

No. OF RECORDS	FIRST GENERATION F <sub>1</sub> #55		FIRST GENERATION F <sub>1</sub> #60		SECOND GENERATION F <sub>2</sub> #60		BACK-CROSS TRISTIS II × F <sub>1</sub> #60	
	191		192		362		284	
	N	%	N	%	N	%	N	%
CHARACTER								
0. NO. OF FLOWERS								
One	40	21.5	12	6.8	88	26.4	65	22.9
Two	89	47.9	75	42.6	168	50.5	156	54.9
Three or More	57	30.6	89	50.6	77	23.1	63	22.2
1. HEIGHT/LENGTH								
Plus	10	5.3	45	27.3	64	17.8	97	33.9
Minus	180	94.7	120	72.7	296	82.2	189	66.1
2. FLOWER SIZE								
$\frac{1}{2}$ " to 1"	5	2.8	19	10.9	50	14.6	0	0
$1\frac{1}{8}$ " to $1\frac{5}{8}$ "	75	43.1	84	48.0	196	57.1	32	12.0
$1\frac{3}{4}$ " to $2\frac{1}{4}$ "	89	51.3	72	41.1	91	26.5	184	68.9
$2\frac{3}{8}$ " to $2\frac{7}{8}$ "	5	2.8	0	0	6	1.8	51	19.1
Statistical Average		1.76		1.62		1.54		2.14
P. E. Average		.02		.05		.01		.01

TABLE 1—Continued

No. OF RECORDS	FIRST GENERATION F <sub>1</sub> #55		FIRST GENERATION F <sub>1</sub> #60		SECOND GENERATION F <sub>2</sub> #60		BACK-CROSS TRISTIS MIX F <sub>1</sub> #60	
	191		192		302		284	
	N	%	N	%	N	%	N	%
CHARACTER								
3. COLOR OF FLOWER								
Creamy	62	32.4	117	61.6	117	32.3	121	42.3
Creamy White	113	59.2	68	35.8	147	40.6	125	43.7
All Others	16	8.4	5	2.6	98	27.1	40	14.0
4. SHAPE OF FLOWER								
Open	121	63.7	62	33.9	115	32.0	248	86.7
Intermediate	7	3.7	24	13.1	39	10.8	17	6.0
Bell	62	32.6	97	53.0	206	57.2	21	7.3
5. TUBE LENGTH								
$\frac{1}{2}$ " to 1"	40	30.8	29	38.7	104	36.6	15	8.5
$1\frac{1}{8}$ " to $1\frac{1}{2}$ "	81	62.3	45	60.0	168	59.2	76	42.9
$1\frac{5}{8}$ " to 2"	9	6.9	1	1.3	12	4.2	83	46.9
$2\frac{1}{8}$ " to $2\frac{5}{8}$ "	0	0	0	0	0	0	3	1.7
Statistical Average	1.29		1.22		1.23		1.60	
P. E. Average	.02		.04		.01		.01	
6. TUBE SHAPE								
Curved	15	39.2	50	64.9	122	43.6	109	60.9
Straight	79	60.8	27	35.1	158	56.4	70	39.1
7. SEGMENT TIP								
Pointed	169	88.5	130	88.7	317	87.8	283	99.3
Blunt	22	11.5	15	10.3	44	12.2	2	.7
8. SEGMENT WIDTH								
Narrow	26	13.7	46	34.8	101	28.2	165	58.3
Intermediate	9	4.7	22	16.7	76	21.2	43	15.2
Wide	155	81.6	64	48.5	181	50.6	75	26.5
9. PETAL TEXTURE								
Wavy	112	59.3	99	61.5	206	57.4	164	57.7
Plain	77	40.7	62	38.5	153	42.6	120	42.3
10. FLOWER COLOR GRAINING								
Plus	134	70.9	91	49.7	171	47.2	15	6.0
Minus	55	29.1	92	50.3	191	52.8	234	94.0
11. FLOWER COLOR BLOTCH								
Plus	174	91.6	119	62.0	258	71.3	209	74.1
Minus	16	8.4	73	38.0	104	28.7	73	25.9
12. FLOWER LINES TO TIP								
Plus	150	78.9	143	78.1	234	64.8	146	51.2
Minus	40	21.1	40	21.9	127	35.2	139	48.8
13. THROAT LINES								
Plus	122	64.6	66	50.8	225	62.3	251	88.1
Minus	67	35.4	64	49.2	136	37.7	34	11.9
14. THROAT DOTS								
Plus	171	90.5	76	58.5	205	56.8	91	32.0
Minus	18	9.5	54	41.5	156	43.2	193	68.0

TABLE 1—Continued

No. of RECORDS	FIRST GENERATION F <sub>1</sub> #55		FIRST GENERATION F <sub>1</sub> #60		SECOND GENERATION F <sub>2</sub> #60		BACK-CROSS TRISTIS II × F <sub>1</sub> #60	
	N	%	N	%	N	%	N	%
CHARACTER								
15/16. TYPES OF FRAGRANCE								
Non-fragrant	4	2.0	7	3.7	135	37.3	111	39.1
Recurvus Scented	185	97.0	182	94.8	188	51.9	53	18.7
Lemon Scented					2	.5	2	.7
Pungent Scented					18	5.0		
Tristis Scented	2	1.0	1	.5	6	1.7	90	31.7
Recurvus and Tristis			2	1.0	8	2.2	17	6.0
Tristis and Lemon					3	.8	3	1.0
Tristis—Day and Night					2	.6	8	2.8
17. ANTHOR COLOR								
Colored—Plus	183	96.3	139	80.3	215	59.7	168	59.2
Pale—Minus	7	3.7	34	19.7	145	40.3	116	40.8
18. PISTIL COLOR								
Colored—Plus	130	85.5	5	3.2	48	14.8	28	9.9
Pale—Minus	22	14.5	153	96.8	277	85.2	255	90.1
19. PISTIL LENGTH								
Plus Anthers	38	43.2	11	26.2	87	35.8	76	54.3
Equal Anthers	41	46.6	26	61.9	112	46.1	53	37.8
Minus Anthers	9	10.2	5	11.9	44	18.1	11	7.9
20. LEAF NUMBER								
One	36	61.0	129	73.3	265	73.4	186	65.5
Two	23	39.0	45	25.6	93	25.8	98	34.5
Three or more			2	1.1	3	.8		
21. LEAF SECTION								
Cross—Plus	30	15.8	18	9.8	52	14.4	235	82.5
Intermediate	147	77.4	152	83.6	253	70.1	50	17.5
Flat—Minus	13	6.8	12	6.6	56	15.5		
22. LEAF COLOR								
Greyish-Green	181	94.8	158	96.3	328	91.1	71	25.1
Yellowish-Green	10	5.2	6	3.7	32	8.9	212	74.9
23. LEAF SHEATH COLOR								
Brown	169	89.4	150	89.8	270	77.4	159	56.8
Intermediate	15	7.9	14	8.4	61	17.5	100	35.7
Green	5	2.7	3	1.8	18	5.1	21	7.5
24. LEAF SHEATH DOTS								
Plus	190	99.5	164	98.2	239	68.5	133	46.8
Minus	1	.5	3	1.8	110	31.5	149	53.2

Of the twenty-five characters treated in table 1, most of them appear to be either heterozygous in the parents of the plants studied, or so irregular in their distribution that they do not indicate any definite trend. The most promising characters are those for fragrance, which show con-

sistent and clear-cut results. These are analyzed more fully in table 2.

The parent of series #60, *Recurvus* Bronze, appeared to be heterozygous for character 4, shape of flower; character 8, segment width, narrow and intermediate being opposed to wide; character 10, flower color grain- ing; character 13, throat lines; and character 14, throat dots. In each of these instances, the parent of series #55, the more typical *Recurvus* Violet Purple, seems to be more homozygous, judging by the  $F_1$  hybrids studied.

For characters 17, 21, 22, 23 and 24, the results in all of the different groups appear much more consistent. Characters 23 and 24 show distributions such as would point to simple dominance of one factor for each.

Taking up the characters a little more fully:

0. The two parent forms of *Recurvus* and *Tristis* II, each have two to four flowers per spike, and the hybrids average two flowers each.
1. The ratio of height of flower stalk to length of longest leaf is consistently negative, and follows the tendency of *G. recurvus*, which is short stalked, while *G. tristis* is long.
2. *Tristis* II is large flowered, averaging  $2\frac{1}{2}$  inches in diameter, while *Recurvus* averages  $\frac{3}{4}$  to 1 inch. The hybrids are intermediate.
3. The flower color is predominantly creamy white, leaning toward the color of *G. tristis*.
4. *Tristis* II is distinctly a wide open flower, while *Recurvus* is more bell shaped. The hybrids are again intermediate.
5. A long perianth tube, 2 inches long, is a character of *Tristis* II, while *Recurvus* Bronze and *Recurvus* Violet Purple both average about  $\frac{3}{4}$  inch. The hybrids are intermediate.
6. The curvature of the perianth tube is highly variable, and shows no clear inherited tendency, except that *Tristis* is curved.
7. The pointed segments of *G. tristis* are strongly epistatic over the blunt segments of *Recurvus*.
8. Wide segments, more than half as wide as long, are characteristic of *Recurvus* in contrast with the narrower segments of *Tristis* II. If narrow and intermediate are contrasted with wide, and *Recurvus* Bronze is assumed to be heterozygous for one of two dominant factors for wide, *Tristis* II and *Recurvus* Violet Purple being homozygous for wide and for narrow segments respectively, the distribution found closely approximates what would be expected, which is 100% wide in  $F_1$  #55, 50% wide in  $F_1$  and in  $F_2$  #60, and 75% intermediate and narrow in the back-cross.

9. The perianth of *Tristis* II is plain, not wavy or ruffled, while that of *Recurvus* is inclined to be wavy, and this tendency slightly predominates in the hybrids.
10. *Tristis* II has a clear color, without markings. *Recurvus* is usually grained and stippled with darker color over the cream or creamy white ground color. In this case, both of the *Recurvus* parent forms appear to be heterozygous for the character for graining, *Recurvus* Bronze the more so.
11. Dark blotches on the three upper segments are characteristic but not invariable in *G. tristis*. *Tristis* II lacks blotches, and *Recurvus* in all its forms has narrow center lines or none. Despite this, blotches appear to preponderate in all groups.
12. Dark central lines to the tips of the segments of the flowers are characteristic of *Recurvus* Violet Purple, and most *Recurvus*, but do not occur in *Tristis* II. The tendency for these lines is evidently somewhat heterozygous in both forms of *Recurvus*. The back-cross shows a typical 1:1 ratio, possibly indicating this character to be a simple dominant.
13. The lower lip of *Tristis* II has greenish central lines in the throat, while *Recurvus* does not. No definite tendency can be detected in this case.
14. Dark dots on the lower lip at the throat characterize most forms of *Recurvus*; *Tristis* II lacks dots. *Recurvus* Bronze is evidently heterozygous for this character, which, from the distribution shown in table 1, and the linkages to characters for fragrance, discussed later, is assumed to depend on two supplementary dominant factors.
- 15 & 16. These characters refer to fragrance. Under 15 are recorded "day-scented" flowers. These include (1) violet scented flowers, with a fragrance like *Recurvus* by day, which are strongly dominant in the first generation, but do not appear in the  $F_2$  and back-cross in the proportions expected for a simple dominant factor; (2) Lemon scented, appearing among the  $F_2$  and back-cross, both alone and in combination with *Tristis* scent at night. This is evidently a derived scent, not found in either of the wild forms used, and is too scantily represented here to permit analysis of its inheritance. (3) Pungent scent, mildly resembling that of a carnation, is another derived scent, and found to the number of 18 (5%), only in the  $F_2$ , neither in  $F_1$  nor back-cross. This would seem to argue for an affiliation with *Recurvus* scent. Under 16



are recorded "night-scented" flowers, which have the strong lily-like scent of *G. tristis* either alone or combined with other scents by day. This character is distinctly recessive in the  $F_1$ , and less represented in the  $F_2$  and back-cross than would be expected of a simple recessive allelomorph to *Recurvus* scent. The proportions of these scents among the different groups, and the large number of non-fragrant hybrids in the  $F_2$  and back-cross, though derived from scented parents and grandparents, exclude the possibility of these traits being inherited either as allelomorphs or as simple independent characters. In the next section an hypothesis is presented which successfully accounts for all of the findings. Discussion of this will be deferred until that is taken up.

17. Dark-colored anthers are characteristic of *Recurvus*, and while *Tristis* II had pale anthers, dark color in them is frequent in other forms of *G. tristis*. Anther color is dominant in the  $F_1$ , but only to the extent of 80% in the  $F_1$  #60. If we may assume both *Recurvus* Bronze and *Tristis* II to be heterozygous for a dominant factor for anther color, this would quite reasonably account for the findings, except for the absence of it in *Tristis* II.
18. *Recurvus* Violet Purple had a violet colored pistil, and this character was evidently dominant in the  $F_1$ . *Recurvus* Bronze and *Tristis* II both had pale pistils.
19. *Tristis* II has the pistil longer than the anthers, and *Recurvus* has it shorter. The hybrids are intermediate.
20. The number of fully developed leaves per plant is normally two in *Tristis* II, but one in *Recurvus*; and the one-leaf predominates in the hybrids.
21. The leaf cross-section is cruciate in *Tristis* II, but flat in *Recurvus*. The hybrids are quite definitely intermediate, except the back-cross, which leans strongly toward the *Tristis* form.
22. *Tristis* II has a normal bright yellowish-green leaf color while *Recurvus* has greyish-green, which is dominant in the  $F_1$ , just as strongly represented in the  $F_2$ , but only 25% are greyish-green in the back-cross. The genetic explanation of this type of distribution is not clear.
23. The color of the leaf sheath is brown in both *Tristis* II and both clones of *Recurvus*, so would be expected to dominate the hybrids.
24. The leaf sheath of *G. recurvus* is characteristically dotted with pale greyish dots on a basic green or brown color. This dotting

is apparently a simple dominant over the uniform sheath color of Tristis II, the two  $F_1$  series being dotted 98 and  $99\frac{1}{2}\%$  respectively;  $68\frac{1}{2}\%$  dotted in the  $F_2$ , approaching a 3:1 ratio; and 47% dotted in the back-cross, nearly a 1:1 ratio, as expected for a one-factor dominant. None of the other characters show such a simple relationship. But the characters for fragrance show interesting trends, which are next considered in detail.

#### INHERITANCE OF FRAGRANCE

If it is assumed that two supplementary factors, designated for convenience R and S, either or both of which may be heterozygous, are necessary to develop recurvus fragrance; that two other supplementary factors, located on different chromosomes and designated T and U, are both necessary, one heterozygous and the other homozygous, to develop tristis fragrance; and that recurvus fragrance is epistatic to tristis fragrance in certain combinations; and further that lemon and pungent are combinations containing tristis fragrance factors; then this hypothesis will account within 2 per cent of error, in all except the first generation, for all of the results given in table 2, which compares the actual inheritance distribution with the computed values based on these assumptions.

Tristis II would then have the genetic formula  $rrssTTUU$ , and Recurvus the formula  $RRSSttuu$ , with respect to fragrance alone. The small letters,  $r, s, t$  and  $u$  represent the non-fragrant allelomorphic factors to the fragrance factors,  $R, S, T$  and  $U$ , respectively. In the hybrids, all having at least one R and one S will also have recurvus fragrance; and those having one T with two U's will have tristis fragrance. But it is further assumed that recurvus fragrance is epistatic to tristis fragrance to such a degree that in the presence of both R and S, homozygous T as well as homozygous U is necessary to bring out both recurvus and tristis fragrances in one individual. Thus  $RrSsTTUU$ , or  $RRSsTTUU$ , or  $RrSSTTUU$ , or  $RRSSTTUU$  would carry both recurvus fragrance by day and tristis fragrance at night. But  $RrSsTtUU$  would show only recurvus fragrance, despite the fact that individuals with  $TtUU$  without R and S together would have tristis fragrance, as would all those with  $TTUU$ , regardless of R and S. The computed values in Table II are based on this hypothesis.

The possibility that the ten percentage values, for recurvus scent in two groups of first generation hybrids, of non-fragrant, recurvus scented, recurvus and tristis scented, and of tristis scent with other combinations, would all except two fall within two per cent of the expected percentages, and that even these divergent values would not deviate more than 4 per cent from those expected, without the hypothesis being true, seems very

TABLE 2

*Comparison of inheritance of recurvus and tristis fragrance with expected values based on two factors for each*

	FIRST GENERATION		FIRST GENERATION		SECOND GENERATION		BACK-CROSS	
	F <sub>1</sub> #55 Tristis II × Recurvus, V. P. 191		F <sub>1</sub> #60 Tristis II × Recurvus, bronze 192		F <sub>2</sub> #60 F <sub>1</sub> #60 × F <sub>1</sub> #60 362		Tristis II × F <sub>1</sub> #60 284	
No. of Plants recorded								
Column A—Actual %								
Column C—Computed %	A	C	A	C	A	C	A	C
1. Non-fragrant	2	0	3.7	0	37.3	35½	39.1	37½
2. Recurvus scented	97	100	94.8	100	51.9	52¾	18.7	18¾
3. Recurvus and Tristis	0	0	1.0	0	2.2	3½	6.0	6½
4. Tristis scented	1	0	.5	0	1.7	*	31.7	*
5. Lemon scented	0	0	0	0	.5	*	.7	*
6. Pungent scented	0	0	0	0	5.0	*	0	*
7. Lmon and Tristis	0	0	0	0	.8	*	1.0	*
8. Tristis, day and night	0	0	0	0	.6	*	2.8	*
* Total, Tristis, Lemon and Pungent combined					*8.6	*8¼	*36.2	*37½

\* Note: These totals are of items 4 to 8 inclusive; Tristis, Lemon, Pungent and combinations of these.

remote. With from two hundred to four hundred individuals recorded in each group, a deviation of 2 per cent from the calculated values is about the normal variability. There seems, therefore, to be no need to assume a more complex or a very different hypothesis from the one proposed to account for the inheritance of the two primary types of fragrance. This explanation does not account for the lemon and pungent scents, except to place them with the tristis group.

#### RELATION OF OTHER CHARACTERS TO FRAGRANCE

To see if there were any indications of linkage of any of the twenty-three other characters to fragrance, all of the data of second generation and later hybrids, (excluding the first back-cross to tristis, Group #152) comprising in all 852 individuals were tabulated with respect to fragrance, and presence or absence of each of the twenty-three other characters, and the material was summarized, showing percentage of the plants possessing a given type of fragrance which also possess a given other character. Then the coefficient of contingency<sup>5</sup> for each of the most strongly probable re-

<sup>5</sup> See, Davenport, C. B. and Ekas, M. P. Statistical Methods, 4th Revised Edition, John Wiley & Sons, 1936.

lations was worked out. The detailed results are not presented here, as they did not prove significant for the present study, except that nine characters numbers 4,6,8,10,12,14,21,22 and 24, (see discussion of table 1 for detailed description of these) showed a strong coefficient of contingency, exceeding .100 in value, for a relationship of the other character to tristis or recurvus fragrance. It is noteworthy that in each of these instances, in every case the porportion of individuals with a given fragrance which also have the character is high, sixty to ninety per cent (see table 3), but the converse of this is not true—that is, of the total number possessing the apparently linked character, the proportion also possessing the fragrance is always less than fifty per cent. To test the significance of these apparent relationships, and to find whether they may represent true linkages between the other characters and fragrance, the 852 indivuals were subdivided into six inheritance groups, designated studies 1 to 6 respectively, as follows:

- Study #1 N—362 Second Generation Tristis II  $\times$  Recurvus Bronze
- Study #2 N—173 Second Generation of #152 (Back-cross to Tristis)
- Study #3 N—74 Second  $\times$  Third Generation of #152
- Study #4 N—54 Second Back-cross to Tristis (Tristis  $\times$  #152)
- Study #5 N—62 Cross between First and Second generation
- Study #6 N—127 Cross between First and Second Generation of Back-cross #152

A portion of this material and a small amount of scattered supplemental data was then lumped into two groups, one consisting of individuals with equal contibutions of *G. tristis* and *G. recurvus* to their pedigrees, and a second group in which all of the individuals have a preponderance of *G. tristis* in their pedigree, as follows:

Group I. Revised study #1 comprises 362  $F_2$  #60.

Individuals and study #5 comprises 62 individuals of a cross  $F_1$  #55  $\times$   $F_2$  #60, making a total of 424 individuals.

Group II. Derivatives of the Tristis back-cross #152 crossed with each other and with other groups, consists of 374 individuals.

Group I is thus equally *G. tristis* and *G. recurvus* in inheritance, while Group II is  $\frac{5}{8}$  or more *G. tristis* and shows strong dominance of *G. tristis* characters.

Any apparent linkage of one character with another may be influenced by dominance of that character, so that two dominant characters may appear to be linked with each other when they really are not. In such instances, if the linkage does not persist in back-crosses in which either or both characters are relatively less frequent, then the apparent linkage is believed not to be significant.

The results of these groupings are given in table 3. In column 1 are

given the characters by number, as described earlier, column 2 gives a statement of the premise for a linkage, columns 3 and 4 give data for the total of 852 cases; in column 3 the norm, that is the percentage of the total group possessing the given character and in column 4 the percentage of the scented individuals also possessing the other character. Thus on line 1, column 3, 51.6 means 51.6 per cent of the individuals in the total group have open shaped flowers, and in column 4 the 79.0 means 79.0 per cent of the individuals with tristis scented flowers in this group also have open flowers. Columns 5 and 6 give similar data for Group I, and columns 7 and 8 for Group II.

TABLE 3

*Linkage of other characters to tristis and recurvus fragrance*

CHARACTER NO.	FINDINGS	TOTAL GROUP N-852 C.		GROUP I STUDY #5 REVISED STUDY #1 N-424 C.		GROUP II STUDY #2-3-6 N-374 C.	
		NORM	%	NORM	%	NORM	%
4	Tristis Scented Flowers ARE OPEN SHAPED	51.6	79.0	30.8	28.6	71.4	82.5
	Recurvus Scented Flowers ARE BELL SHAPED	32.9	50.8	56.4	59.1	10.3	15.2
	Coefficient of Contingency	.374		.017		.175	
6	Tristis Scented Flowers ARE CURVED TUBED	55.3	66.7	45.1	57.1	61.7	70.5
	Recurvus Scented Flowers ARE STRAIGHT TUBED	44.7	51.1	54.9	55.2	38.3	38.6
	Coefficient of Contingency	.161		.051		.095	
8	Tristis Scented Flowers ARE NARROW PETAL	43.8	70.9	27.9	42.8	56.7	69.9
	Recurvus Scented Flowers ARE WIDE PETAL	34.7	51.6	51.3	54.7	20.0	39.1
	Coefficient of Contingency	.409		.096		.395	
10	Tristis Scented Flowers LACK GRAINING	68.3	96.5	52.4	85.7	82.3	96.8
	Recurvus Scented Flowers ARE GRAINED	31.7	49.0	47.6	50.5	17.7	43.5
	Coefficient of Contingency	.378		.131		.444	
TRISTIS FRAGRANCE		N 86	10.1	N 67	1.7	N 63	16.9
RECURVATUS FRAGRANCE		N 252	29.6	N 204	48.1	N 47	12.6

TABLE 3—Continued

CHARACTER NO.	FINDINGS	TOTAL GROUP		GROUP I STUDY #5 REVISED STUDY #1		GROUP II STUDY #2-3-6	
		N-852 C.	%	N-424 C.	%	N-374 C.	%
12	Tristis Scented Flowers LACK LINES TO TIP	50.6	61.6	35.9	14.3	63.5	60.3
	Recurvus Scented Flowers HAVE LINES TO TIP	49.4	60.6	64.1	65.2	36.5	41.3
	Coefficient of Contingency	.191		.075		.017	
14	Tristis Scented Flowers LACK THROAT DOTS	55.2	80.2	45.2	85.7	60.2	74.6
	Recurvus Scented Flowers HAVE THROAT DOTS	44.8	63.3	54.8	62.7	39.8	67.4
	Coefficient of Contingency	.354		.177		.386	
21	Tristis Scented ARE CROSS LEAF	46.5	89.5	15.8	42.9	74.7	92.1
	Recurvus Scented ARE INTERM. OR FLAT LEAF	53.5	81.1	84.2	84.7	25.3	47.7
	Coefficient of Contingency	.538		.172		.346	
22	Tristis Scented ARE GREEN LEAVED	28.1	54.7	11.1	28.6	44.8	55.6
	Recurvus Scented ARE GRAY LEAVED	71.9	90.7	88.9	92.6	55.2	81.4
	Coefficient of Contingency	.418		.141		.346	
24	Tristis Scented LACK SHEATH DOTS	46.2	63.1	30.0	42.9	58.4	59.0
	Recurvus Scented HAVE SHEATH DOTS	53.9	69.5	70.0	75.3	41.6	45.5
	Coefficient of Contingency	.279		.068		.046	
TRISTIS FRAGRANCE		N 86	10.1	N 7	1.7	N63	16.9
RECURVUS FRAGRANCE		N252	29.6	N204	48.1	N47	12.6

In table 3 is shown the linkage of other characters to tristis and recurvus fragrance expressed by means of a coefficient of contingency. Character 21—Leaf Section—shows the strongest linkage to fragrance (C. = .538) and table 4 shows in detail how this coefficient of contingency was computed.



TABLE 4

*Note: Selections made from a total group of 852 hybrids.*

	TRISTIS FRAGRANCE	RECURVUS FRAGRANCE	
Cross Leaf Section	77	47	124
Intermediate and Flat Leaf Section	9	202	211
	86	249	

$$\frac{1}{86} \left( \frac{5929}{124} + \frac{81}{211} \right) = .5599$$

$$\frac{1}{249} \left( \frac{2209}{124} + \frac{40804}{211} \right) = .8480$$

$$P = 1.4079$$

$$\sqrt{\frac{.4079}{1.4079}} = \sqrt{.2897} = C = .538$$

In order to determine the coefficient of contingency we had to obtain first a measure of probability called P from the square contingency, which may be interpreted by means of a coefficient of contingency. The most valuable form is that derived by Pearson, which he has called  $C_2$  or which we may call C. In its interpretation C is identical with the "product moment coefficient of correlation." It should be particularly noted that if we employ only two classes as the established means of our coefficient of contingency the highest possible coefficient may be only .707; table 4 therefore clearly shows that the relationship; tristis scented flowers are cross-leafed and Recurvus, scented flowers are intermediate or flat-leafed, is a valid one.

A comparison of linkage of these characters to tristis and to recurvus fragrance, expressed as percentage of the total tristis or recurvus fragrant hybrids possessing the character shows as follows:

Character 4. Flower Shape, shows in Group I a relationship of bell shape of flower to recurvus scented—59.1 per cent; both of these characters are strongly represented in this group, but only 15.2 per cent of the recurvus scented are bell shaped in Group II, which is predominantly open rather than bell shaped. The apparent linkage in Group I is reversed in Group II. Tristis scented flowers in Group II show 82.5 per cent open shaped flowers, only 28.6 per cent however in Group I. The apparent relationship of 79 per cent for the total group is not borne out in both sections of it. Accordingly we can only assume there is no consistent linkage of flower shape to either tristis or recurvus fragrance.

Character 6, flower tube curvature, is by similar reasoning to the above, weakly related, curved tube to tristis scented, in Group II 70.5 per cent. Group I, with very few tristis scented plants, shows 57.1 per cent of tristis scent with curved tube. But the converse, straight tube to recurvus scent shows no relationship.

Character 8, narrow petaled, are represented amongst tristis scented 69.9 per cent in Group II, and 42.8 per cent in Group I, which has few of narrow petaled and still fewer tristis scented. Again the converse relationship to recurvus scent is not found.

Character 10, darker graining on the petals, fails to show relationship to recurvus fragrance, being nearly half and half, with and without graining in Group I, Group II and the Total Group. But the absence of graining is strongly represented among the tristis scented plants, 96.8 per cent in Group II, 85.7 per cent in Group I and 96.5 per cent in the Total Group.

Characters 12, 21, and 24 all show reversals in apparent relationships in the two groups, with regard to tristis and recurvus fragrance.

Character 14, throat dots on the lower lips of the flower, also show a weak relationship, 62.7 per cent and 67.4 per cent in the two groups respectively, while the converse shows even a closer relationship and linkage, 85.7 per cent and 74.6 per cent respectively.

Character 22, leaf color, shows close relationship of recurvus scent to gray leaf 92.6 per cent and 81.4 per cent respectively but none of tristis to green leaf.

Thus of the nine characters showing a 60 per cent or greater apparent linkage to tristis or recurvus fragrance in the Total Group, only four of them, nos. 6, 10, 14 and 22 show this consistently in Groups I and II. Let us consider the minimum group relationship as most nearly the true one—and this is reasonable, since in breeding with this material, selection of parents was entirely for fragrance, the other characters not being given any consideration, so that they may be regarded as random selections with regard to all except fragrance.

Then tristis scent may be regarded as linked to curved tube (character 6) 57.1%, and to lack of graining (character 10) 85.7%. In each of these cases no converse relationship to recurvus fragrance is found. This further supports the hypothesis already stated that the factors for tristis and for recurvus scent are not allelomorphs. But in the case of character 14, tristis scented lack throat dots 74.6%, and recurvus scented have throat dots 62.7%, thus showing an apparent relationship to each fragrance. If throat dots are dependent on two dominant factors, so that the absence of throat dots is linked to one factor for tristis and the presence

of them is linked to one for recurvus fragrance, it would then fulfill the requirements in this instance. By reference to table 1 the proportion of throat dots found in the first and second generations and back-cross would fit in well with this assumption also, if we assume that the parent of  $F_1$  #55, i.e. Recurvus Violet Purple, is homozygous for each of two factors for throat dots, but that the parent of  $F_1$  #60, Recurvus Bronze, is homozygous for one factor for throat dots, but heterozygous for the other. Grey leaved is apparently linked to recurvus scented, recurvus scented being grey-leaved (character 22) 81.4%, but not tristis scented to green leaved.

The relationship of tristis scented to other characters in Group I is insecure in each case, being based on only seven tristis scented individuals, but the other relationships, based on 47, 63 and 204 individuals respectively, may be regarded as reasonably sure.

#### CONCLUSION

1. From a study of hybrids of *G. tristis* with *G. recurvus* consisting of  $F_1$ ,  $F_2$  and a back-cross of  $F_1 \times$  tristis, it was found that the violet-like fragrance of *G. recurvus* was dominant, and the aromatic night scent of *G. tristis* was recessive.

2. In the  $F_2$  and the back-cross two new types of fragrance were observed and designated lemon scented and pungent scented.

3. From a study of the proportions of each type of fragrance and combinations of them in the different groups of hybrids, and from the occurrence of large proportions of scentless  $F_2$  and back-cross hybrids it is assumed that each primary type of fragrance is a resultant of the influence of two independent genetic factors, such that two dominant factors are necessary for the expression of recurvus scent, and a dominant and recessive factor for the expression of tristis scent.

4. A preliminary survey of the relationships of the other recorded characters to those for fragrance indicate that the factors for curved flower tube, and for absence of graining of dark color on the flowers are linked each to one factor for tristis scent, that the factors for spotted throat of the flower are linked to both tristis scent and recurvus scent, and that grey leaf color is strongly linked to recurvus scent.

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## Studies in Onagraceae XI. A revision of the genus *Gaura*

PHILIP A. MUNZ

(concluded)

### 11. *GAURA BRACHYCARPA* Small, *Flora S.E. U. S.*, 848, 1335. 1903.

Apparently a winter annual, branched at base, the stems simple or again branched, very slender, decumbent, 1-3.5 dm. long, finely hirsute in leafy part; rosette-leaves oblanceolate, 4-6 cm. long, remotely sinuate-dentate, obtuse, gradually narrowed into short winged petioles, somewhat villous; cauline leaves on lower half of stems, the blades thin, mostly lance-ovate, sinuate-denticulate to subentire, 1.5-4 cm. long, 5-12 mm. wide, acute to obtuse, somewhat cuneate, sparsely villous, sometimes linear-lanceolate; spikes few-flowered, slender, strigulose, somewhat peduncled, nodding at tip, 5-20 cm. long; hypanthium strigulose, slender, 4-7 mm. long, copiously white-pubescent within; sepals 6-8 mm. long, strigulose, linear, reflexed separately in anthesis; petals white, aging pink, spatulate, 6-8 mm. long; stamens subequal, filaments flattened, 4-5 mm. long, with basal scale; anthers reddish, ca. 2 mm. long; style pubescent at base, somewhat surpassing stamens; stigma-lobes about two-thirds mm. long; capsule elongate-pyramidal, 5-7 mm. long, subglobose, flat at base, 4-angled, the angles auricled at base, the faces transversely wrinkled; seeds few.

Type locality, San Diego, Texas. Ranging rather widely in eastern Texas. Representative material, TEXAS: Dallas, *Reverchon in 1874* (G); 6 mi. northwest of Valley Springs, Llano Co., *Cory 6269* (P); San Marcos, Hayes Co., *Stanfield in 1897* (NY); West Cave, Blanco Co., *Bogusch 713* (US); San Antonio, *Jermy 254* (NY), *Clemens 687* (P); Sutherland Springs, Wilson Co., *Jones in 1932* (P); Corpus Christi, Nueces Co., *Heller 1391* (G, NY, US); Kingsville, Kleberg Co., *Jones 29568* (P); Sabinal, Uvalde Co., *Jones in 1932* (P); Carrizo Springs, Dimmit Co., *Jones 28141* (P); Laredo, Webb Co., *Palmer 11264* (G, NY, US); San Diego, Duval Co., *Croft 109*, type (NY).

This species is characterized by its slender decumbent stems, its strigulose buds, and pyramidal auricled fruit.

### 12. *GAURA TRIPETALA* Cav., *Icones* 4: 66, pl. 396. 1797.

Apparently annual to short-lived perennial, usually branched from base stems rather slender, simple or branched, ascending, hirsute, often reddish, 2-6 dm. long; basal leaves oblanceolate, sinuate-dentate, 4-8 cm. long, narrowed into short winged petioles, more or less pubescent, especially on veins and margins; cauline leaves lanceolate to oblong-linear, entire to sinuate-

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dentate, sometimes wavy, almost or quite sessile, 2–5 cm. long, almost glabrous to pubescent, acuminate to obtuse; spikes 1–3 dm. long, somewhat peduncled; hypanthium 4–5 mm. long, slender, often reddish, pubescent within; sepals 3, narrow, 4–6 mm. long, usually distinct in anthesis; petals 3, oblanceolate, 3–4 mm. long, red in age; stamens 6, subequal; filaments 3–4 mm. long; anthers often red, 1–1.5 mm. long; style pubescent at base; capsule ovoid-pyramidal, sharply 3-angled, 4–8 mm. long, each face with median rib and transverse wrinkles.

## KEY TO VARIETIES

Inflorescence glandular-pubescent. Hidalgo to Puebla..... 12a. *G. tripetala* var. *typica*  
 Inflorescence not glandular.

Buds strigose. Texas to Durango..... 12b. *G. tripetala* var. *Coryi*

Buds glabrous. Oklahoma..... 12c. *G. tripetala* var. *triangulata*

12a. *Gaura tripetala* Cav. var. *typica* n.nom.

*G. tripetala* Cav., Icon. 4: 66, pl. 396. 1797. *G. hexandra* Ortega, Hort. Matr. Dec., 14, 1797; Sessé & Moc., Pl. N. Hispan., ed. 1, 56. 1887-'90.

Inflorescence, hypanthium, calyx and ovary glandular-puberulent.

Type locality, "Prope Pachuca et San Agustin," Hidalgo, Mex. Ranging in central Mexico. Material seen, WITHOUT LOCALITY: *G. tripetala* ex herb. Madrid, A. Gray, 1880 (G); Jard. des Plantes, in 1815 (G); Mexico, Ruiz (Ber, photos at G, P); *G. hexandra*, Sessé, Mociño, Castillo, & Maldonado 5147 & 936 (Madrid) FEDERAL DISTRICT; Tultenango, Rose & Painter 7840 (US); Eslava, Rusby 123 (NY), Rose & Painter 7145 (G, US); valley of Mexico, Pringle 9795 in part (G, US); Toluca, Berlandier 1099 (US); Ixtaccihuatl, Purpus in 1903 (US). PUEBLA: Rte. de Cholula, Puebla, Arsène 900 (NY, US); Cerro et fort de Guadalupe, Arsène in 1908 (NY, US); Laguna de San Baltasar, Arsène 1113 (US).

12b. *G. tripetala* Cav. var. *Coryi* n.var.

Hypanthium, sepals, usually ovaries strigulose. (Hypanthium, sepala, et plenunque ovaria strigulosa).

Type, dry banks, Hempstead, Waller Co., Texas, E. Hall 211, April 25, 1872, Pomona College Herbarium No. 39283; isotypes (G, NY, US). Texas and northern Mexico. Representative material, TEXAS: without locality, Wright 205 (G, US), Drummond III, 82 (NY); Bryan, Brazos Co., Palmer 7794 (NY, US); Encino (Encinal?), La Salle Co., Jones 29567 (P); near San Angelo, Tom Green Co., Cory 8824 (P); Olney, Young Co., Cory 13142 (P). MEXICO: without locality, Coulter 163 (G); Aguascalientes, Rose & Painter 7786 (NY, US); Saltillo, Gregg 29 (G); La Quemada, Zacatecas, Seler 4790 (G); Durango, E. Palmer 257, in 1896 (G, NY, US). It is a pleasure to name this new variety for my friend Mr. V. L. Cory of



Sonora, Texas, who has done so much interesting work in recent years on the flora of his state.

12c. *Gaura tripetala* Cav. var. *triangulata* (Buckl.) n. comb.

*G. triangulata* Buckl., Proc. Acad. Sci. Philad. 1861: 454. 1862.

Hypanthium, calyx, and ovaries glabrous.

Type locality, "Prairies Northern Texas," May, S. B. Buckley. I have seen the following material, OKLAHOMA: Cache, Comanche Co., *Stevens* 1325 (G, NY); Ft. Sill, Domanche Co., *Clemens* 11709 (G); Catoosa, Rogers Co., *Bush* 1131 (NY); Oklahoma City, *Carleton* 129 (US). An intergrade with var. *Coryi* is: 15 miles east of Tulsa, *Engelman* in 1935 (P).

I am indebted to Dr. Francis Pennell of the Philadelphia Academy for examining and reporting to me on the glabrous condition of Buckley's type.

I should add, before going on to the next species, that I have some mis-giving as to the recognition of *Gaura tripetala* as a species. Its chief claim to specific rank is its tripetalous and trisepalous condition. But after studying *G. angustifolia* and finding flowers on the same plant built on both the plan of 3 and that of 4, I am somewhat dubious as to the value of this character. Furthermore, some sheets referred to *G. tripetala* seem more like one species, others like another. For example, *Palmer* 257 from Du-ango seems very much like *G. gracilis*, while most Texas plants are more like *G. brachycarpa*. I am therefore not at all sure that all are conspecific. However, since in Texas and Mexican material I have seen no such variation in number of floral parts as in the Florida species *angustifolia*, and since without much cytological and garden evidence, further status cannot be determined, I am forced for the present to recognize *G. tripetala*.

13. *GAURA VILLOSA* Torr., Ann. Lyc. N.Y. 2: 200, 1828.

Perennial, usually suffrutescent, stems several from base, ascending-erect, mostly 5-10 dm. tall, with several divergent lateral leafy branches closely placed and at a distance of 2-3 dm. above the base, often with another similar umbellate group further up the stem; stems canescent or rather stiffly appressed-villous; leaves numerous, crowded, canescent, appressed-villous, more or less undulate, the lower ones spatulate to ovate or lanceolate, mostly sinuate-serrate or -denticulate, acuminate to obtuse, 3-7 cm. long, 8-25 mm. wide, narrowed at base, subsessile or short-petioled, upper ones linear to lance-ovate, 1.5-2 cm. long, 3-15 mm. wide; floral bracts ovate to ovate-lanceolate, 1-3 mm. long caducous, pubescent at least on the margins; inflorescence 3-6 dm. long, open, branched, with very slender stems, scarcely peduncled, the branches subglabrous, occasionally cinereous-strigulose; hypanthium funnel-form, 2 mm. long, with dense white curly pubescence within; sepals lance-

linear, 7–10 mm. long, separate in anthesis; petals white, turning red, ca. 8 mm. long, broadly elliptic, abruptly narrowed into slender claw ca. 2 mm. long; stamens subequal, filaments 8–9 mm. long, slightly enlarged upward; anthers 2–3 mm. long, red; style slightly exceeding stamens, pubescent at base; stigma-lobes ca. 0.3 mm. long; capsule usually finely puberulent, sometimes subglabrous, the body oblong, wing-angled, somewhat narrowed toward summit, 7–9 mm. long, 2–3 mm. wide, rather abruptly narrowed into a very slender stipe-like base 3–6 mm. long.

## KEY TO VARIETIES

Hypanthium and sepals cinereous-strigulose.

Ovary cinereous-strigulose; leaves canescent-villous. Kansas to Texas. .... 13a. *G. villosa* var. *typica*

Ovary quite glabrous except for few hairs near the summit. So. Texas. .... 13b. *G. villosa* var. *McKelveyae*

Hypanthium, sepals and ovary with short spreading hairs.

Hairs of hypanthium, etc. not gland-tipped. So. Texas. .... 13c. *G. villosa* var. *Parksii*

Hairs of hypanthium, etc. gland-tipped. Western Texas & E. New Mex. .... 13d. *G. villosa* var. *arenicola*

13a. *Gaura villosa* Torr. var. *typica* n.var.

*G. villosa* Torr., Ann. Lyc. N. Y. 2: 200. 1828. *G. cinerea* Woot. & Standl., Contr. U. S. Nat. Herb. 16: 152. 1913.

Leaves canescent-villous, the lower lanceolate to spatulate, 8–15 mm. wide, the upper 3–5 mm. wide; hypanthium, sepals, ovaries cinereous-strigose.

Type locality, "Sources of the Canadian," the original collection by James. Range New Mex. and Kans to Texas. Representative material, NEW MEXICO: 20 miles south of Roswell, Chaves Co., *F. S. & E. S. Earle* 533, type coll., cinerea (NY, US); Santa Rosa, Guadalupe Co., *Degener* 4803 (NY); sources of the Canadian, *James*, type villosa (NY). KANSAS: Morton Co., *Hitchcock* 172 (G, NY, US); Arkalon, Seward Co., *Smyth* 157 (NY, US); Coldwater, Comanche Co., *Rydberg & Imler* 678 (NY); Meade, Meade Co., *Smyth in 1890* (NY). OKLAHOMA: False Washita, bet. Ft. Cobb & Ft. Arbuckle, *Palmer* 137 (NY, US); Alva, Woods Co., *Stevens* 773 (G, NY, US); Clinton, Custer Co., *Palmer* 12549 (G, NY, US); Bridgeport, Caddo Co., *Munz* 13576 (P). TEXAS: Seymour, Baylor Co., *Reverchon* 10 (G, NY); Estelline, Hall Co., *Reverchon* 4306 (G, P, US); Posey Canyon, Lubbock Co., *Demaree* 7767 (G); 16 miles no. of Matador, Motley Co., *Cory* 16046 (P); near Wellington, Collingsworth Co., *Cory* 16144 (P).

13b. *G. villosa* Torr. var. *McKelveyae* n.var.

Strictly herbaceous; stems decumbent, then ascending, 3–5 dm. long; leaves deeply and regularly sinuate-dentate, oblong-lanceolate to oblanceolate

in outline, sparsely villous, about as wide as in *typica*, but seeming narrower because of the deeper dentation; hypanthium and sepals cinereous-strigulose; ovary usually glabrous except for a few hairs near the summit. (Planta herbacea; caulibus decumbentibus, tunc ascendentibus, 3-5 dm. longis; foliis sinuato-dentatis, parce villosis; hipantio sepalisque cinereo-strigulosis; ovario plerumque glabro, cum capillis paucis supra.)

Type, near Mathis, San Patricio Co., Texas, April 5, 1931, *Susan Delano McKelvey 1718*, Gray Herbarium; isotype Pomona 186535. Other material seen, TEXAS: Corpus Christi, *Tracy 9273* (G, NY, US); Hidalgo Co., *Runyon 153* (US); near Brownsville, Cameron Co., *Townsend 32* (US). It is a great pleasure to name this very distinct, more herbaceous, less villous local plant of extreme southern Texas for Mrs. McKelvey, whose collections of Onagraceae from Texas have been of great help to me.

13c. *Gaura villosa* Torr. var. *Parksii* n.var.

Leaves densely soft-silky, lanceolate to ovate, the lower 10-25 mm. wide, the upper 5-15 mm. wide; hypanthium, sepals, and ovary with dense grayish short spreading hairs. (Folia sericea, lanceolata aut ovata, infimis 10-25 mm. latis, superioribus 5-15 mm. latis; hipantio, sepalis, et ovario cum capillis curtis et extensis.)

Type, sandy open places, Terrell Hill, near Kaicaster, Wilson Co., Texas, June 24, 1935, *P. A. Munz 13334* Pomona College Herbarium 212450; isotypes 212582, 212583, 212449. Other material seen, TEXAS: sandy plains of the Nueces, *Wright in 1848* (G); Stonewreath Hills, Lower Rio Grande, *Schott* (NY); 17 miles so. of San Antonio, *Metz 656* (NY); near Devine, Medina Co., *Cory 12736* (P); San Ygnacio, *Tharp 3622* (US); east of Carrizo Springs, Dimmit Co., *Jones 28140* (P).

This interesting variant was first pointed out to me in the field by Mr. H. B. Parks, botanist and entomologist of San Antonio, Texas, and I am very happy to name it for him.

13d. *Gaura villosa* Torr. var. *arenicola* n.var.

Leaves densely soft-silky, lanceolate to lance-ovate, 5-10 mm. wide; hypanthium, sepals, and ovary with short spreading gland-tipped hairs. (Folia sericea, lanceolata aut lanceo-ovata, 5-10 mm. lata; hipantio, sepalis et ovario cum capillis curtis, extensis et glandulosis).

Type, five miles northeast of Portales, Roosevelt Co., New Mexico, on sand dunes near Highway 33, June 14, 1930, *Goodman & Hitchcock 1124*, Pomona College Herbarium No. 171881; isotype at NY. Other material seen, NEW MEXICO: near Portales, *Wootton in 1909* (US). TEXAS: sand hills, 2 mi. so. of Muleschoc, Bailey Co., *Ferris & Duncan 3421* (NY);

Odessa, *Reed* 1909 (US); 2 miles west of Bledsoe, Morton Co., *Cory* 16528 (P) OKLAHOMA: Canadian River Valley, near Pack Saddle Bridge, Ellis Co., *Goodman* 2591 (P).

14. *GAURA FILIPES* Spach, Nouv. Ann. Mus. Paris 4: 379. 1835.

Perennial herb, branched from base, 5–18 dm. tall, ascending to erect, the stems puberulent, sometimes also hirsute, reddish, paniculately branched above; basal leaves not seen; cauline leaves numerous, crowded on lower parts of stem, linear to oblanceolate or lanceolate, usually sinuate-denticulate 3–6 cm. long, 3–15 mm. wide, acute to obtuse, narrowed at base, subsessile or short-petioled, subglabrous to strigulose, sometimes villous underneath on veins; upper leaves reduced, 0.5–2 cm. long, lance-linear, acuminate; floral bracts lance-linear, 3–5 mm. long, caducous; inflorescence open-paniculate, 2–5 dm. long, canescent-strigulose especially on the buds, scarcely peduncled or with peduncles 5–10 cm. long, the spikes on very slender axes; hypanthium gray-strigulose without, narrow-funnelform, 3–5 mm. long, white-puberulent within; sepals strigulose, lance-linear, 5–10 mm. long, reflexed separately in anthesis; petals white, turning rose, broadly oblanceolate, clawed, 4–6 mm. long; filaments subequal, slightly enlarged upward, 4–5 mm. long; anthers 1.5–2 mm. long; style pubescent at base, scarcely exceeding stamens; stigma-lobes 0.4–0.8 mm. long; capsule strigulose, obovoid-clavate, sharply 4-angled toward the summit, the body 4–5 mm. long, scarcely 2 mm. wide, gradually or rather abruptly narrowed into a very slender pedicel-like base 1–3 mm. long.

KEY TO VARIETIES

Sepals 5–7 mm. long; petals 4–5 mm. long.....14a. *G. filipes* var. *typica*  
Sepals 8–10 mm. long; petals 6 mm. long.....14b. *G. filipes* var. *major*

14a. *Gaura filipes* Spach var. *typica* n.var.

*G. filipes* Spach, Nouv. Ann. Mus. Paris 4: 379. 1835.

Flowers small; sepals 5–8 mm. long; petals 4–5 mm. long.

Type locality, Jacksonville, Fla. Range from So. Car. to Fla. Representative material, SOUTH CAROLINA: 25 miles west of Columbia, Lexington Co., *Munz* 13359 (P); Aiken, *Ravenel* (NY, US); Clemson College, *House* 2894 (US). GEORGIA: Cobb Co., *Wilson in* 1900 (G, NY, US); Hogansville, Troup Co., *Wiegand & Manning* 2166 (G). ALABAMA: Auburn, Lee Co., *Earle & Baker* 1230 (NY, P); Mobile, *Mohr* (G). MISSISSIPPI: Meridian, *Schuchert in* 1896 (US). FLORIDA: Aspalaga, *Curtiss* 3929c (G, NY, US); River Junction, Gadsden Co., *Nash* 2578 (G, NY, US); Jacksonville, *Drummond*, apparently type coll. (G, K, photo at P); Lake City, *Nash* 2498 (US).

- 14b. GAURA FILIPES Spach var. MAJOR Torr. & Gray, Fl. N. Am. 1: 517. 1840.

*G. Michauxii* Spach, Nouv. Ann. Mus. Paris 4: 379. 1835.

Flowers larger, the sepals 8-10 mm. long; the petals 6 mm. long.

Type locality, Kentucky, if we use as type the first specimen cited which was collected by Short. Specimens seen, INDIANA: 1 mi. west of Plainsville, Daviess Co., *Deam 47902* (G, US). TENNESSEE: Lookout Mt., *Biltmore Herb. 3929b* (G, NY, US); Cowan, Franklin Co., *Biltmore Herb. 3929a* (G, NY, US). KENTUCKY: Barrens of Ky, *Short*, type (NY). Without definite locality, "Chez les Cherokees, *Palisot de Beauvois*, type *Michauxii* (Del, photo at P). Material from Jackson Co., Fla., *Chapman* (NY) is quite intermediate in flower size with var. *typica*. A peculiar specimen ("On shell islands near Gulf," La., *Langlois 97* (NY) has capsule and stipe of *G. filipes* and flower-size of *G. Lindheimeri*; it may possibly be a hybrid of *Lindheimeri* and some other.

15. GAURA NEALLEYI Coulter, Contrib. U. S. Nat. Herb. 1: 38. 1890.

Apparently mostly biennial from a fleshy tap root, usually several-stemmed from base, sometimes simple; stems hirsute below, mostly simple, ascending to erect, 2-6 dm. high; basal leaves oblanceolate, sinuate-dentate, 5-15 cm. long, 8-18 mm. wide, quite glabrous except for the short stiff hairs on margins and beneath the midrib, narrowed gradually into a winged petiole; lower cauline leaves rather crowded, lanceolate, almost sessile, sinuate-dentate, acute, with pubescence of basal leaves, mostly 1.5-3 cm. long, 5-10 mm. wide; uppermost reduced and almost linear; floral bracts rounded-ovate, ciliate, 2.5-3.5 mm. long, caducous; inflorescence rather few-flowered, lax spicate, scarcely or short-peduncled, becoming 1-3 dm. long in fruit, subglabrous in lower parts, glandular-puberulent in upper parts and on hypanthium and calyx and ovary; hypanthium 8-12 mm. long, puberulent within; sepals 8-11 mm. long, reflexed separately in anthesis; petals whitish, aging red, broadly oblanceolate, 4-5 mm. long; stamens subequal; filaments 4-5 mm. long, somewhat flattened; anthers 2-3 mm. long; style exceeding stamens, puberulent at base; stigma-lobes ca. 0.6 mm. long; capsules ovoid-pyramidal, 8-9 mm. long, 2.5-3 mm. wide, rather sharply 4-angled, glabrous, each face with midrib and minute transverse wrinkles, the base abruptly narrowed into a thick stipe-like base 1-1.5 mm. long.

Type locality, Chenate Mts., Presidio Co., Texas. Range, western Texas and adjacent New Mexico. Material seen, TEXAS: Limpia Canyon, 12 mi. north of Ft. Davis, Jeff Davis Co., *Cory 9659* (P), Limpia Canyon, *Tracy 294* (G, NY), Limpai Creek, *Earle & Tracy 294a* (NY, US); Davis Mts., *Earle & Tracy in 1902* (NY); Old Ft. Davis, *Ferris & Duncan 2718*

(NY); Cibolo, *Havard in 1881* (US); Chenates region, *Nealley in 1889*, type (US); Kokernot Springs, near Alpine, Brewster Co., *Cory 9632* (P). NEW MEXICO: Dark Canyon, Guadalupe Mts., *Standley 40666* (US); Copper Mines, *Wright in 1851* (NY); El Capitan Mts., Lincoln Co., *F. S. & E. S. Earle 517* (NY, US).

This species is characterized by its hirsute stem, glandular inflorescence, and short stipe. It intergrades with *G. gracilis* f. *glandulosa* from which it is doubtfully distinct. For example, of the specimens above cited, *Cory 9632* approaches the latter in its very short stipe; *Long 7437* (US) from Sandia Mts., New Mex. has the short stipe of *gracilis* but the flowers of *Nealleyi*. *Nelson 3913* (US) from La Ventura, Coahuila has the flower size of *Nealleyi* but the strigulose fruit of typical *gracilis*.

16. GAURA SINUATA Nutt., ex Seringe, in DC., Prodr. 3: 44. 1828.

Perennial herb, 3–8 dm. tall, the stem simple or more generally with several ascending branches from above the base, glabrous or nearly so; basal leaves oblanceolate to oblong-lanceolate, subglabrous, or puberulent especially on the edges, 3–8 cm. long, 1–2 cm. wide, sinuate-dentate, obtuse to acute, with short winged petioles; cauline leaves rather crowded, spatulate to lanceolate, even linear, sinuate-dentate to almost entire, often wavy, subglabrous to strigulose, 1–5 cm. long; floral bracts 1–3 mm. long, caducous, lanceolate to ovate with narrow tip, subglabrous or with few short hairs on margins; inflorescence simple or branched, 2–5 dm. long, with naked peduncles 1 or more dm. long; hypanthium 2.5–3 mm. long, subglabrous or sparsely strigulose, narrow-funnelform, white-pubescent within; sepals grayish-strigulose, 7–10 mm. long, narrow, separately reflexed in anthesis; petals white, becoming red, 8–10 mm. long, broadly elliptic, the claw rather narrow, ca. 2 mm. long; filaments subequal, slightly enlarged upward, 8–10 mm. long; anthers reddish 3–3.5 mm. long; style somewhat longer than stamens, puberulent at very base; stigma-lobes about 0.5 mm. long; capsule nearly or quite glabrous, the body fusiform, obtusely 4-angled, 5–9 mm. long, 1–1.5 mm. wide, gradually tapering into rather thick pedicel-like base 2–5 mm. long.

Type locality, "In Arkanza et Red-River," probably in Okla. Ranging from Okla. to northern Mexico. Representative material, Arkansas & Red River, *Nuttall in 1825*, type coll. (Del), Arkansa, *Nuttall* (Kew, photo at P); Red River, *Nuttall* (NY). OKLAHOMA: Mountain Park, Kiowa Co., *Stevens 1218* (G, P); Granite, Greer Co., *Stevens 999* (G, NY, US); Mannsville, Johnston Co., *Griffith 3491* (G, NY); Norman, Cleveland Co., *Middleton in 1935* (P). TEXAS: Texas III, *Drummond 76* (G, NY); Chilithe, Wilbarger Co., *Ball 961* (NY, US); Ft. Worth, *Ruth 37* (G, NY, US); Dallas, *Reverchon*, Curtiss distrib. 896 (G, NY); Mertzon, Irion Co., *Palmer 12415* (G, NY, US); Comanche Spring, *Lindheimer 800* (G, US);



Kerrville, Kerr Co., *Heller* 1692 (G, NY, US); New Braunfels, *Lindheimer* 802 (G, NY, US); New Hempstead, Waller Co., *Hall* 214 (G, NY, P); Carrizo Spring, Dimmit Co., *Jones* 28145 (P); Refugio, Refugio Co., *Benke* 5401 (P); Limpio, *Wright in* 1851 (G); Kingsville, Kleberg Co., *Tracy* 9275 (NY, US); Diversion Lake, Archer Co., *Cory* 13222 (P). COAHUILA: Diaz, *Pringle* 8320 (G, NY, P, US); Saltillo, *Palmer* 233 (G, NY, P, US); Sabinas, *Nelson* 6810 (US). TAMAULIPAS: Cerro del Chino, Sierra de San Carlos, *Bartlett* 10717 (US).

This species is characterized by its slender, pedicelled glabrous fruit. It is becoming naturalized out of its original range, as for example, So. Car., Charleston, *Robinson* 196 (G); Tuscaloosa, Ala., *Harper* 3192 (NY, US); San Dimas, Los Angeles Co., California, *Wheeler* 947 (P); junction Los Troncos and San Francisco Creeks, San Mateo Co., Calif. *Abrams* 13687 (P).

17. GAURA ODORATA Sessé ex Lagasca, Gen. et Spec. Pl., 14. 1816.

*Schizocarya Drummondii* Spach, Nouv. Ann. Mus. Paris IV, 3: 382. 1835. *Gaura Drummondii* T. & G., Fl. N. Am. 1: 519. 1840; D. Dietr., Syn. Pl., 1297. 1840. *G. hispida* Benth., Pl. Hartweg., 288. 1840.

Apparently biennial or winter annual, mostly branched at base, the stems ascending, 2-5 dm. high, rather slender, simple or few-branched, grayish pubescent, the hair appressed or spreading but usually not over 1 mm. long; basal leaves apparently oblanceolate, sinuate-dentate; lower stem leaves lanceolate to ovate or oblanceolate, 2-5 cm. long, 5-15 mm. wide, sinuate-dentate, acutish at both ends, scarcely petioled, rather crowded, gradually reduced upward and becoming lance-linear, strigulose; floral bracts lance-ovate, acute, 3-6 mm. long, strigulose, caducous; spikes sessile or short-pedunculate, with nodding tips, 1-3 dm. long in fruit, mostly strigulose; petals oblong-lanceolate, 8 mm. long, white to pink, turning red; stamens subequal, filaments flattened, 5-6 mm. long; anthers reddish, ca. 4 mm. long; style well exerted beyond stamens, pubescent at base; stigma-lobes ca. 1 mm. long; capsule glabrous to strigulose, 8-11 mm. long, the lower third terete, gradually enlarged upward, the upper two-thirds ovoid-pyramidal, acute, rather sharply 4-angled, each face ca. 2.5 mm. wide, with median nerve; seeds up to 4.

Type locality, "Habitat in Nova Hispania." Ranging from Texas to central Mexico. Representative material, TEXAS: Ft. Worth, *Ruth* 276 (NY); Comanche Spring, *Lindheimer* 41 (G); Temple, Bell Co., *Wolff* 3016 (US); San Felipe de Austin, *Drummond* 36, type coll. *Drummondii* (G, NY, K, photo at P); Austin, *Hall* 213 (G, NY, P, US); near Roosevelt, Kimble Co., *Cory* 18969 (P); San Antonio, *Heller* 1590 (G, NY, US); Bracken, Bexar Co., *Groth* 146 (G, NY, US); Uvalde, *Palmer* 13530 (US); San Diego, Duval Co., *Croft* 111 (NY). TAMAULIPAS: Matamoros,

*Berlandier* 2313 (G). NUEVO LEON: Monterey, *Dodge* 110 (US). COAHUILA: Saltillo, *Palmer* 23 (G, NY, US); DURANGO: Durango, *Palmer* 94 (G, NY, US). GUANAJUATO: Leon, *Hartweg* 1603, type *hispida* (K, photo at P). SAN LUIS POTOSI: Guascama, *Purpus* 5383 (G, NY, US). MICHOACÁN: Morelia, *Arsène* 2752 (G, US). QUERÉTARO: Querétaro, *Arsène* 10599 (G, US). HIDALGO: Ixmiquilpan, *Rose, Painter and Rose* 9079 (G, US). PUEBLA: San Luis Tultitlanapa, *Purpus* 3387 (G, NY, US). OAXACA: Distr. Etla, *Seler* 83 (G, US); Huitzo, *Rose & Rose* 11364 (G, NY, US). Without locality, "*G. odorata* Lag., Hort. veg. Matrit 1814? Reuter (Boissier)."

I am unable to separate plants with hirsute stems from those without; nor can I find any other definite characters by which *G. hispida*, for instance, can be segregated from the other material. Plants from the more southern and western parts of the range seem to have more pubescence on the fruits than do others. The species is with some difficulty separable from all forms of *G. coccinea*, which also has the thick base to the fruit, but I believe the larger flowers and more early shedding of the floral bracts, as well as usually longer fruits generally distinguish the two.

18. *GAURA COCCINEA* Nutt. ex Fraser's Cat., 1813 as *nomen nudum*; ex Pursh, Fl. Sept. Am. 2: 733. 1816; Nutt., Gen Am. 1: 249. 1818.

Perennial herb; stems several, simple or branched, ascending, 1–5 dm. high glabrous to strigose and hirsute; leaves numerous, mostly sessile, the lower oblanceolate to broadly or narrowly lanceolate or oblong, 1.5–3.5 cm. long; main ones oblong-lanceolate to almost linear; uppermost linear to lance-linear; leaves canescent to glabrous; floral bracts linear to lanceolate, 3–6 (11) mm. long, persistent; spikes simple, sessile or short-peduncled, becoming 5–18 cm. long, nodding at tips; hypanthium narrow-infundibuliform, 5–8 mm. long, strigulose without, puberulent within; sepals oblong-linear separately reflexed in anthesis, 5–8 mm. long; petals whitish to pink or red, aging red, 3–6 mm. long, broadly elliptic with narrow claw; stamens subequal; filaments 4–5 mm. long, white to yellowish, somewhat flattened upward; anthers yellow or red, 2–5 mm. long; style slightly exceeding stamens, pubescent at base; stigma-lobes suborbicular, ca. 0.25 mm. long; capsule 5–10 mm. long, 1.5–3 mm. thick, sessile, the body proper 4-angled, tapering toward the tip in pyramidal fashion, abruptly constricted toward the gradually narrowed but stout terete base.

#### KEY TO VARIETIES

Capsule 5–7 mm. long, 2.5–3 mm. wide; anthers 2–3 mm. long.

Stem and leaves more or less pubescent.

Leaves (at least the lower) lanceolate and sinuate-dentate.

Main leaves mostly plane, oblong, crowded; flowers crowded; inflorescence not peduncled; plant 1–3 dm. high. Ariz. and New Mex. northward. . . . 18a. *G. coccinea* var. *typica*

- Main leaves mostly waved and crisped, acutish, not crowded; flowers not crowded; inflorescence with short peduncle; plant 3-4 dm. high. Ariz. and Texas to Mexico. . . . . 18b. *G. coccinea* var. *epilobioides*  
 Leaves linear, subentire. . . . . 18c. *G. coccinea* var. *parvifolia*  
 Stem and leaves glabrous. . . . . 18d. *G. coccinea* var. *glabra*  
 Capsule ca. 10 mm. long, 1.5-2 mm. wide; anthers 4-5 mm. long. Rare, Ariz. to Coahuila. . . . . 18e. *G. coccinea* var. *arizonica*

18a. *Gaura coccinea* Nutt. var. *typica* n.nom.

*G. coccinea* Nutt. ex Pursh, Fl. Sept. Am. 2: 733, 1816. *G. multicaulis* Raf., Atlanti. Journ., 146. 1832 new name for *coccinea*. *G. marginata* Lehm., in Hook., Fl. Bor. Am. 1: 208. 1834. *G. coccinea* var. *integerrima* Torr., Ann. Lyc. N. Y., 2: 200. 1828. *G. Roemeriana* Scheele, Linnaea 21: 579. 1848.

Stems canescent-strigose, mostly 1-3 dm. high, more or less hirsute; leaves canescent, oblong to lanceolate, 4-8 mm. wide (the upper narrower), repand-dentate to entire, 1-3.5 cm. long; spikes mostly dense not more than 1 dm. long, usually not peduncled.

Type locality, "from the Missouri." Ranging widely from Alberta and Manitoba to eastern Calif., Ariz. and Texas. Representative material, ASSINIBOIA: Regina, *Fowler in 1903* (US). ALBERTA: Rosedale, *Moodie 1024* (G, NY, US); Medicine Hat, *Macoun 4937* (G). SASKATCHEWAN: Moose Jaw, *Johnson in 1905* (NY). MINNESOTA: Lake Traverse, Traverse Co., *Sheldon in 1893* (G, NY, US). NORTH DAKOTA: Leeds, Benton Co., *Lunelli in 1910* (NY, US); Mandan, *Sarvis 22* (US). SOUTH DAKOTA: Deadwood, *Carr 51* (G, NY, US); Jamesville, *Bruce in 1899* (US). MONTANA: Pony, Madison Co., *Rydberg & Bessey 4589* (G, NY, US); Great Falls, *Wilcox 16* (NY); Helena, *Kelsey in 1891* (P). WYOMING: Buffalo, Johnson Co., *Tweedy 3621* (NY); Dayton, Sheridan Co., *Tweedy 2604* (NY). UTAH: Towner's Ranch, *Purpus 6161* (P). NEVADA: Las Vegas, Clark Co., *Rydberg 6255* (NY); Indian Spring, *Jones in 1906* (P). CALIFORNIA: Providence Mts., e. San Bernardino Co., *Munz, Johnston & Harwood 4058* (P, US); Barnwell, *Munz 13837* (P). ARIZONA: Williams, *Toumey 160* (US); Flagstaff, *MacDougal 205* (G, NY, US); Peach Springs, *Wilson in 1893* (NY, US); Ft. Huachuca, *Wilcox in 1891* (US). COLORADO: Ft. Collins, *Crandall in 1896* (NY); Galeton, Weld Co., *Johnston 1017* (P); Sterling, Logan Co., *Mathias 335* (P); Denver, *Clokey 2779* (NY); Pueblo, *Baker, Earle & Tracy 9* (NY, P, US); Buena Vista, Chaffee Co., *Keck 848* (P); Silverton, *Tweedy 110* (US). KANSAS: Logan Co., *Hitchcock 171* (G, NY, US); Johnson, Stanton Co., *Thompson 70* (G, NY, US); Dodge City, *Ellis in 1891* (NY, US). NEBRASKA: Thedford, Thomas Co., *Rydberg 1343* (NY, US); Broken Bow, *Webber in 1889* (NY, US); Ogalalla, *Jones in 1925* (P). MISSOURI: Watson, Atchison Co., *Bush 333* (G, NY, US); Atherton, Jackson Co.,

*Bush* 7977 (NY). OKLAHOMA: Cherokee, Alfalfa Co., *Stevens* 647 (G, NY, US); Huntsville, Kingfisher Co., *Blankinship in 1896* (G, US). NEW MEXICO: sources of the Canadian, *James*, type of var. *integerrima* (NY); Las Vegas, *Arsène* 18788 (P); Sandia Mts., Sandoval Co., *Ellis* 117 (NY, US); Datil, Catron Co., *Eggleston* 20345 (NY, US); Silver City, Grant Co., *Eastwood* 8442 (G). TEXAS: Limpia Canyon, Davis Mts., *Tracy & Earle* 295 (G, NY, US); Cienega Mt., Brewster Co., *Cory* 2147 (P); Del Rio, Val Verde Co., *Palmer* 11351 (G, NY, US); Neubraunfels, *Roemer*, Prager Herb. (Calif. Acad.) type coll. *Roemeriana*. It has been naturalized in various places outside its native range: Bingen, Wash., *Suksdorf in 1903* (NY); Brea, Orange Co., Calif., *Wolf* 3809 (NY); Idaville, White Co., Ind., *Deam* 48855 (G); Rochester, Mich., *Farwell* 7017 (G); Rochester, N.Y. *Baxter* 1007 (G); Porto Alegre, Rio Grande do Sul, Brazil, *Reinick in 1899* (G).

18b. *Gaura coccinea* Nutt. var. *epilobioides* (HBK) n.comb.

*G. epilobioides* HBK., Nov. Gen. et Sp. 6: 93. 1823. *Schizocarya Kunthii* Spach, Nouv. Ann. Mus. Paris 4: 383. 1835 new name for *epilobioides*. *G. sinuata* Moc. & Sessé ex Ser., in DC., Prodr. 3: 45. 1828, as syn. *G. spicata* Moc. & Sessé ex Ser., l.c. in syn.; Moc. & Sessé, Pl. N. Hispan. ed. 1, 55. 1887-90. *G. suffrutescens* Moc. & Sessé, ex Ser., l.c. *G. bracteata* Moc. & Sessé ex Ser., l.c. *Schizocarya crispa* Spach, l.c., 384. *Gaura crispa* D. Dietr., Syn. Pl., 1298, 1840.

Stems mostly 3-4 dm. long, mostly cinereous-stringose; leaves not crowded, mostly acute to acuminate, cinnereous, 1-3 cm. long, 1.5-4 mm. wide, wavy; spikes 1-2.5 dm. long, lax, often on peduncles up to 4 cm. long.

Type locality, Actopán, Hidalgo, Mexico. Ranging from Arizona and Texas to south central Mexico. Representative material, ARIZONA: Kingman, Mohave Co., *Kearney & Peebles* 12591 (Sacaton); Congress Jct., Yavapai Co., *Jones in 1903* (P, US); 12 mi. no. of White River, Navajo Co., *Goodman & Hitchcock* 1303 (NY, P); Santa Rita Mts., *Pringle* 16 (G); Ft. Huachuca, *Palmer* 417 (G, US). NEW MEXICO: Carlsbad Cavern, *Standley* 40429 (US). TEXAS: Chisos Mts., *Mueller* 8105 (G, NY); Chenati Mts., Presidio Co., *Nealley* 156 (NY, US); Alpine, *Hughes* 31 (NY); San Antonio, *Jermy* (G, NY, US). CHIHUAHUA: Chihuahua, *Palmer* 369 (G, NY, US). COAHUILA: Saltillo, *Palmer* 24, (G, NY, US); DURANGO: Tepehuanes, *Palmer* 275 (G, NY, US). VERA CRUZ: Orizaba, *Botteri* 915 (G). NUEVO LEON: Bawes, *C. H. & M. T. Mueller* 218 (P). ZACATECAS: Concepción del Oro, *Palmer* 308 (G, US). SAN LUIS POTOSI: San Luis Potosi, *Parry & Palmer* 255 (G, US). HIDALGO: Actopán, Humboldt, type coll (Ber, photo at P; apparently

same at Paris); Pachuca, *Rose Painter & Rose*, 8820 (NY, US). MEXICO: Jacaboys, *Pringle* 10397 (G, US); San Angel, drawing of *G. sinuata* fl. mex., *G. bracteata* Ser. (Del, G, P); PUEBLA: Tehuacán, *Seler* 8 (G). Without locality, *G.?* *suffrutescens* Sessé & Mociño, pl. Geneva (Del, tracing G, P); *G. sinuata*, *Sessé, Mociño, Castillo & Maldonado* 5148 & 938 (Madria).

More southern, taller, more lax, with leaves less crowded and more wavy than in var. *typica*, but intergrading freely with it; for example, Flagstaff, Ariz., *Munz* 13001 (P); Oracle, Ariz., *Jones in 1903* (P); Sonora, *Loomis & Peebles* 5351A (Sacaton, US); Bill Bunton's Ranch, Presidio Co., Texas, *Cory* 2141 (P); Kiowa Creek, Sterling Co., Texas, *Cory* 584 (P); Parras, Coahuila, *Gregg in 1847* (G, NY).

18c. GAURA COCCINEA Nutt. var. PARVIFOLIA (Torr.) T. & G., Fl. N. Am. 1: 518. 1840.

*G. parvifolia* Torr., Ann. Lyc. N.Y. 2: 201. 1828. *G. linearis* Woot. & Standl. Contr. U. S. Nat. Herb. 16: 154. 1913.

Branches and leaves subglabrous to pubescent; leaves quite linear, entire mostly 5–15 mm. long, 1–2 mm. wide.

Type locality, "On the Canadian." Ranging from Kansas and Colorado to northern Mexico. Representative material, KANSAS: Kandrado, *Smyth* 459 (NY); Goodland, *Smyth in 1892* (NY); Tribune, Greeley Co., *Reed in 1892* (P). COLORADO: Pueblo, *Popenoe in 1878* (P); NEW MEXICO: On the Canadian *James*, type (NY); Tularosa Creek, Otero Co., *Wooton in 1897* (G, US); Albuquerque, *Jones* 4120 (P); Lakewood, *Wooton in 1909*, type *linearis* (US); Silver City, Grant Co., *Wolf* 2625 (G, P). ARIZONA: Cottonwood, *Rothrock* 349 (G, US); Elgin, So. Ariz., *Peebles, Harrison & Kearney* 3363 (Sacaton); Ft. Huachuca, *Wilcox in 1894* (US). TEXAS: Culberson Co., *Cory* 2142 (P); Red River above Burkburnett, *Tharp* 524 (NY); Vernon, *Reverchren* 3846 (G, US). CHIHUAHUA: San Pedro, Sierra Madre, *Jones in 1903* (P); Casas Grandes, *Nelson* 6336 (US). ZACATECAS: Concepción del Oro, *E. Palmer* 318 (NY).

Intergrading freely with var. *typica*, as for example, Trail Glen, Colo., *Clements* 45 (G, NY); Durango, Colo., *Tweedy* 440 (NY, US); Alpine, Texas, *Cory* 9281 (P), *Palmer* 34029a (NY); Las Vegas, New Mex., *Arsène* 18363 (P); Ft. Bayard, New Mex., *Mulford* 570 (NY); so. of Raton, N. M., *Mathias* 539 (P). Smoother plants intergrade with var. *glabra*: Santa Fé, New Mex., *Bertrand* 66 (US); Dulca, Jicarilla Apache Reservation, *Standley* 8165 (US); San Ysidro, *Arsène* 19012 (US); Ute Park, Colfax Co., New Mex., *Standley* 13866 (US); Seward Co., Kansas, *Carleton* 334

(US); Huachuca Mts., Ariz., *Holzner* 1568 (US); San Francisco Mts., *Knowlton* 175 (US).

18d. GAURA COCCINEA Nutt. var. GLABRA (Lehm.) Torr. & Gray, Fl. N. Am. 1: 518. 1840.

*G. glabra* Lehm. in Hook., Fl. Bor. Am. 1: 209. 1834. *G. induta* Woot. & Standl., Contrib. U. S. Nat. Herb. 16: 153. 1913.

Plant nearly or quite glabrous on stems and leaves; leaves as in var. *typica*, but more wavy; hypanthium strigulose.

Type locality, "About Carlton-House, on the Saskatchewan." With much the same range as var. *typica* and in some regions (Wyo. & Colo.) seemingly more abundant than that variety; perhaps this should be rated as only a form, since its glabrous condition is its chief character, but its tendency toward more wavy leaves may argue for varietal recognition. Material from northeastern New Mexico and eastern Colorado tends to have narrow leaves and is Wooton and Standley's *induta*; it is somewhat intermediate with var. *parvifolia*. Plants from Wyoming and Montana have very blunt and short lower leaves; but intermediate material between these extremes and the usual form is more abundant than any of the extremes themselves. Representative material may be cited as follows, NEBRASKA: Kimball, *Moldenke* 7232 (NY). KANSAS: Tribune, Greeley Co., *Reed* in 1892 (P); Liberal, Seward Co., *Rydberg & Imler* 868 (NY). MONTANA: Ravalli, *Jones* in 1909 (P); Custer, Yellowstone Co., *Lloyd* in 1893 (NY); Pony, Madison Co., *Rydberg & Bessey* 4590 (NY). SOUTH DAKOTA: Ft. Pierce, *Harper* in 1891 (P); Hot Springs, Fall River Co., *Rydberg* 709 (NY, US). WYOMING: Buffalo, Sheridan Co., *Tweedy* 3620 (NY); Platte Hills, *Nelson* 392 (G); Sybille, Albany Co., *Nelson* 7412 (G, NY, P, US); Granger, Sweetwater Co., *Jones* in 1896 (P), *Merrill & Wilcox* 787 (NY, US). COLORADO: Livermore, Larimer Co., *Munz* 11124 (P); New Windsor, Weld Co., *Osterhout* in 1901 (NY, P); Denver, *Jones* 657 (P, US); Gunnison, *Baker* 456 (G, NY, P, US); Trinidad, *Mulford* 10 (NY). UTAH: St. George, Washington Co., *Jones* 5110 (P, US); San Juan River, *Eastwood* 30 (G, US). NEVADA: Las Vegas, *Craig* 1392 (P), *Goodding* 2303 (G, NY). CALIFORNIA: Clark Mt., eastern Mohave Desert, *Munz* 12857 (P). ARIZONA: Prescott, *Wolf* 2348 (G); Hackberry, Mohave Co., *Jones* 4475 (G, NY, P in part, US); Rye, Gila Co., *Jones* in 1890 (P); Ft. Huachuca, *Palmer* 420 (US). NEW MEXICO: Santa Fe, A. A. & E. G. *Heller* 3659 (G, NY, P); White Mts., Lincoln Co., *Wooton* 186 (G, P); Pecos, San Miguel Co., *Standley* 4933, type coll. *induta* (G, NY, US); Farmington, San Juan Co., *Standley* 6919 (US). OKLAHOMA:



Alva, Woods Co., *Stevens 658* (NY, US). TEXAS: El Solitario, Brewster Co., *Cory 2140* (P); near Kirkland, Hardeman Co., *Cory 13366* (P).

18e. *Gaura coccinea* Nutt. var. *arizonica* n. var.

Stems several, 3-6 dm. high, branched, canescent-strigulose, densely leafy; main leaves lanceolate to lance-ovate, wavy, 2-5 cm. long, 3-8 mm. wide; floral bracts lance-linear, 4-12 mm. long; spikes 3 dm. long in fruit; hypanthium cinereous-strigulose, narrow, 6-7 (10) mm. long; sepals cinereous-strigulose, 9-10 mm. long; petals 6 mm. long; anthers 4-5 mm. long; capsule usually cinereous-strigulose, ca. 1 cm. long, 1.5-2 mm. wide, thickest at about the middle, with a rather long-acuminate beak. (Caules 3-6 dm. alti, canescento-strigulosi; foliis lanceolatis aut lanceo-ovatis, undulatis, 2-5 cm. longis; hipantio cinereo-striguloso, angusto, 6-7 (10) mm. longo; sepalis cinereo-strigulosis, 9-10 mm. longis; petalis 6 mm. longis; antheris 4-5 mm. longis; capsulis 1 cm. longis, 1.5-2 mm. latis, rostratis, cinereo-strigulosis).

Type, Globe, Arizona, *Eastwood 8657*, May 17, 1919, Gray Herbarium. Other material seen, ARIZONA: Globe, *Kearney & Peebles 9263* (Sacaton, US), *9262* (Sacaton, US); Marana, Pima Co., *Harrison & Fulton 6817* (Sacaton); between Casa Grande & Tucson, *Harrison 6817* (US); Marana, *Loomis & Peebles* (Sacaton); Prescott, *Peebles, Harrison & Kearney 4288* (Sacaton); Mesa near Rock & Rye Creeks, Gila Co., *Collom 86a* (US). NEW MEXICO: Gallinas River, *Eggleston 5973* (US). COAHUILA: Carneros Pass, *Pringle 3105* (NY, US in part).

Characterized by its long anthers and long narrow capsules, this variety might almost seem to be worthy of specific recognition and it was in that fashion that I first treated it. But it does intergrade with *G. coccinea* var. *glabra*, for example, *Kearney & Peebles 9263* above cited, also *Toumey 144* from Hot Springs, Ariz (US).

UNCERTAIN OR EXCLUDED NAMES

GAURA CHINENSIS Lour., Fl. Coch., 225 1790. The sessile stigma, erect petals and other characters mentioned in Loureiro's description would exclude this yellow-flowered plant from *Gaura*. At the present writing I do not have access to literature on Chinese Botany and do not know what disposition has been made of this name.

GAURA EPILOBIA Moc. & Sesse, ex Ser., in DC., Prodr. 3: 45. 1828 is *Oenothera* (Hartmannia) *rosea* Ait., Hort. Kew. ed. 1, 2: 3. 1789.

GAURA? FRUTICULOSA Benth., Voy. Sulph., 15. 1844 is *Gonglyocarpus fruticulosus* Brandg., Proc. Calif. Acad. II, 2: 158. 1889.

GAURA FRUTICOSA Loefl., Iter Hispan., 248. 1758 is *Combretum fruticosum* Stuntz, U. S. Dept. Agric., Bur. Pl. Ind., Invent. Seeds & Pl. Import. No. 31: 86. 1914.

## Explanation of figures

(This plate is made to illustrate the shapes of the fruits of the various species of *Gaura*. In order to avoid confusion, no shading nor pubescence is indicated). All specimens indicated are in Pomona College Herbarium.)

Fig. 1. *Gaura mutabilis* Cav. Fruit 9 mm. long; Colonia Juarez, Mex., Jones in 1903.

Fig. 2. *Guara parviflora* Dougl. var. *typica*. Fruit 8 mm. long; Shawmut, Mont., C. L. Hitchcock 2441.

Fig. 3. *Gaura biennis* L. var. *typica*. Fruit 6.5 mm. long; Philadelphia, Penn., G. Watson.

Fig. 4. *Gaura neomexicana* Woot. var. *typica*. Fruit 8 mm. long; Tularosa Creek, Otero Co., New Mex., Wolf 2768.

Fig. 5. *Guara macrocarpa* Rothrock. Fruit 14 mm. long; Jeff Davis Co., Tex., Cory 2137.

Fig. 6. *Gaura Lindheimeri* Engelm. & Gray, Fruit 9 mm. long; Houston, Tex., Munz 13339.

Fig. 7. *Gaura angustifolia* Michx. var. *typica*. Fruit 8 mm. long; Ortega, Fla. O'Neill 1011.

Fig. 8. *Gaura filiformis* Small var. *typica*. Fruit 6 mm. long; Dickenson, Galveston Co., Tex., Cory 11398.

Fig. 9. *Gaura suffulta* Engelm. var. *typica*. Fruit 6 mm. long; Live Oak Creek, Crockett Co., Tex., Cory in 1936.

Fig. 10. *Gaura gracilis* Woot. & Standl. var. *typica*. Fruit 7 mm. long; Black Range, New Mex., Metcalfe 1033.

Fig. 11. *Gaura brachycarpa* Small. Fruit 9 mm. long; Sabinal, Tex., Jones 29570.

Fig. 12. *Gaura tripetala* Cav. var. *typica*. Fruit 8 mm. long; Hempstead, Tex., E. Hall 211.

Fig. 13. *Gaura villosa* Torr. var. *typica*. Fruit 13 mm. long; near Romero, Hartley Co., Tex., Cory 16424.

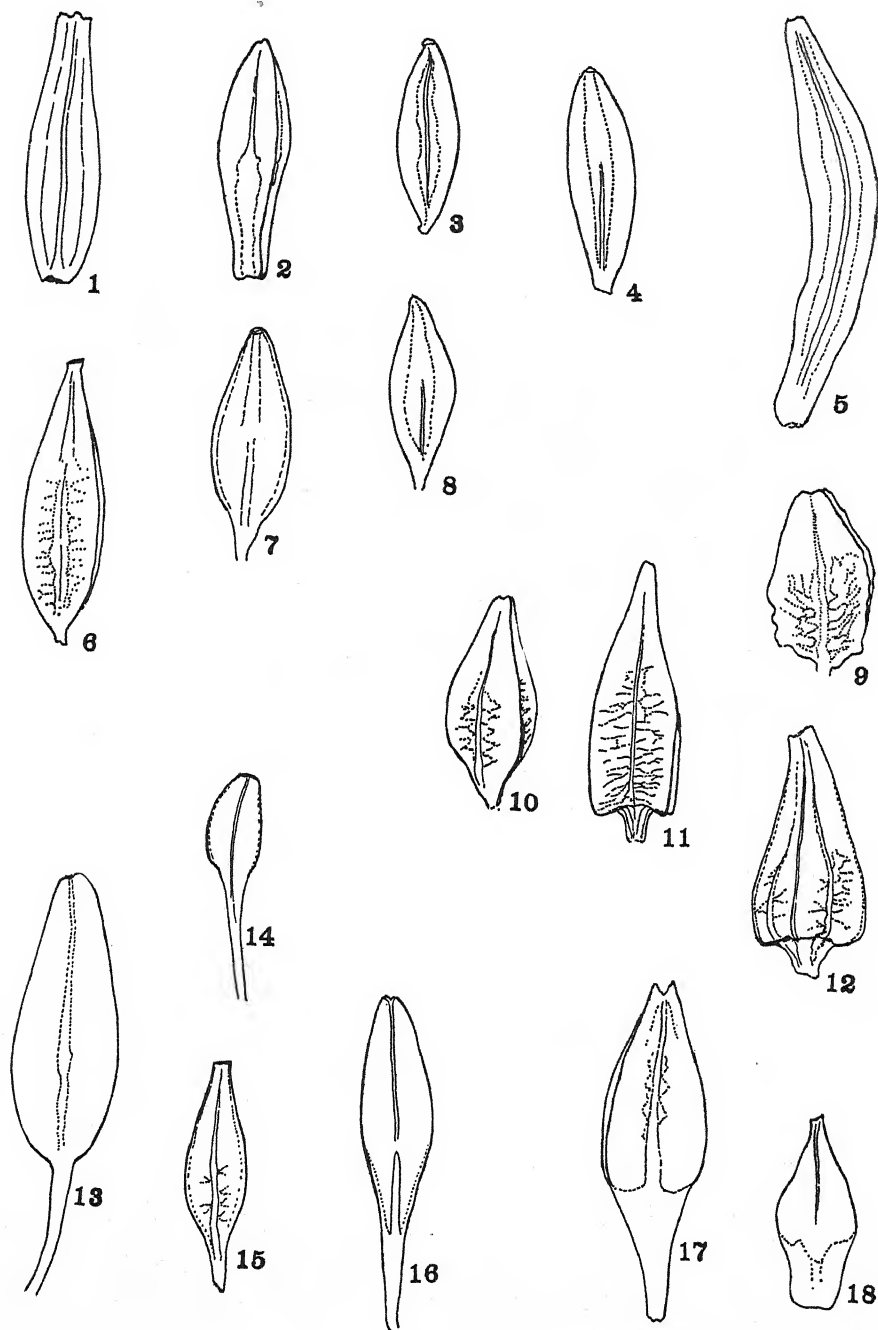
Fig. 14. *Gaura filipes* Spach. var. *typica*. Fruit 8 mm. long; Auburn, Ala., Earle & Baker in 1897.

Fig. 15. *Gaura Nealleyi* Coulter. Fruit 8 mm. long; Limpio Canyon, Tex., Cory 9659.

Fig. 16. *Gaura sinuata* Nutt. Fruit 10 mm. long; Diversion Lake, Archer Co., Tex., Cory 13222.

Fig. 17. *Gaura odorata* Sesse. Fruit 10 mm. long; Austin, Texas, E. Hall 213.

Fig. 18. *Gaura coccinea* Nutt. var. *typica*. Fruit 7 mm. long; Big Lake, Reagan Co., Tex., Cory 585.



Figures 1-18. Explanation on opposite page

GUARA HETERANDRA Torr., Pacif. RR. Rept. 4: 87. 1857 is *Heterogaura heterandra* Cov., Contr. U. S. Nat- Herb. 4: 106. 1893.

GAURA HIRSUTA Scheele, Linnaea 21: 580, 1848. I am uncertain from the description as to application of this name and have been unable to locate the type on which it is based. It may well be *G. Lindheimeri*.

GAURA HUMILIS D. Dietr. Syn. Pl. 2: 1297. 1840 is *Gayophytum humile* Juss., Ann. Sci. Nat. ser. 1, 25: 18. 1832.

GAURA LAXA Loeßl., Iter Hispan., 248. 1758 is *Combretum Loeßlingii* Eichl., in Mart., Fl. Bras. xiv, 2: 110 according to Index Kewensis.

GUARA LEUCOCARPA Comien, ex Steud., Nom., ed. 2, 1: 666. 1840, nomen nudum.

GAURA LINIFOLIA Nutt., ex James, Exped. Rocky Mts., 2: 355, 1823 is *Stenosiphon linifolium* Britton, Mem. Torrey Club 5: 236. 1894.

GAURA UNDULATA Desf., Tableau de l'Ecole de Bot., ed. 2, 196. 1815, nomen nudum.

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## Effect of artificial wind on growth and transpiration in the Italian millet, *Setaria italica*

V. PANDURANGA RAO

(WITH ONE FIGURE)

Wind is one of the potent environmental factors that affect vegetation. Notwithstanding its importance, the literature upon this subject is meager and is largely confined to non-agricultural plants, sugar cane and orchard trees being the chief exceptions. The problem is especially important in those parts of India where moderate to strong winds prevail during the growing period and occasionally contribute to widespread destruction of crops.

The great importance of *Setaria italica* as a food crop for the poorer classes in these semiarid regions makes its behavior toward wind especially interesting.

### MATERIAL AND METHODS

Strain No. K. 23 of *Setaria italica* Beauv., developed at the Dry Farming Station, Bellary, South India, was used in this experiment, which was carried out in the greenhouse at Lincoln, Nebraska, during the summer of 1937.

Moist, screened, fertile and well mixed loess soil was uniformly tamped into eight cylindrical, galvanized iron containers that were 9 inches in diameter, 19 inches deep, and contained one-half inch of gravel. The top of each completely filled container was tightly covered with water-proof oilcloth. A tightly fitting 3-inch cork containing 3 half-inch holes was placed in an opening cut in the center of each cover and sealed with liquid glue to prevent loss of moisture. On June 22, two seeds were planted in the soil just below each of the holes in the corks, the holes filled with sand, and the phytometers weighed.

Five days after germination the seedlings were thinned to three per container, *i.e.*, one per opening. The eight phytometers were arranged in two sets of four each and each set was insulated by wrapping it with several thicknesses of heavy brown paper. One lot of six-day-old seedlings was placed 2 feet from a 16-inch electric fan where a wind velocity of 5 m.p.h. was created when the fan was run from 9 to 11 a.m. and from 3 to 5 p.m. the first day. On the next day, the fan was run from 6 a.m. to 6 p.m., and on the third day at 10 a.m. the wind velocity was increased to 11 m.p.h. until 6 p.m. This latter velocity was then maintained from 6 a.m. to 6 p.m. daily throughout the experiment. The phytometers were restored to their original weight at intervals by addition of water. Detailed notes of the

condition of the plants and of water used were taken. The second lot, in the meantime, was placed under conditions that were similar except for the absence of wind. Loss of water was determined by frequent weighing, enough water being added to replace that transpired.

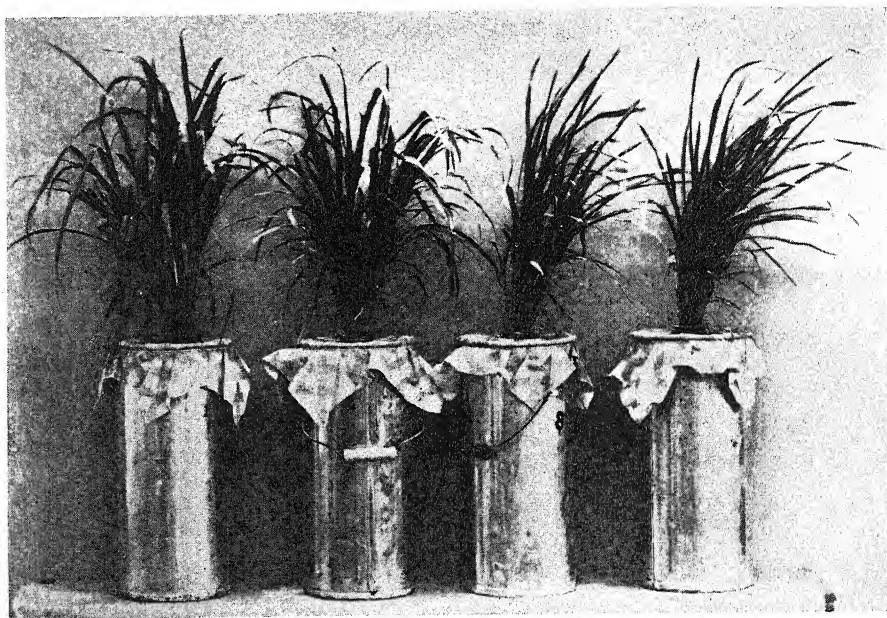


Fig. 1. Two lots of control plants of *Setaria italica* (left) and two groups that have been exposed to wind 12 hours daily.

Average daily evaporation from Livingston's black spherical atmometers was 46.7 cc. near plants exposed to the wind, and 20.7 cc. near the controls. The summer was very warm and temperatures of 100° to 110°F. were frequently attained during the early afternoon, despite the fact that the greenhouse was unusually well ventilated and the glass partly covered with whitewash. The air temperature (of numerous readings made between 10 a.m. and 2 p.m.—97.1°F.) was 3.3°F. lower about the plants in the wind. The light intensity on the treated plants was 6700 foot candles, which was almost identical with that of the controls. The average relative humidity during the experiment, as determined by numerous readings of a cog psychrometer, was 69 per cent.

At the end of a month of treatment, after weighing the phytometers, the shoots were oven-dried at 90°C. for 24 hours and weighed. The containers were placed in a slanting trough, their sides cut open, and the roots, which had nearly reached the bottoms of the containers, were exposed by carefully washing away all the soil with a gentle stream of water. Root



volumes, obtained by displacement of water, and oven-dry weights were secured.

### RESULTS

The effect of the wind became visible on the fifth day when tips and margins of the first three leaves began to dry. Notwithstanding this symptom, the plants continued to grow more vigorously than the controls for the first 13 days of treatment as shown in table 1.

TABLE 1  
*Effect of wind upon the height of Setaria italica.*

AGE OF SEEDLING, DAYS	DAYS AFTER TREATMENT	HEIGHT IN CM.	
		CONTROL (WITHOUT WIND)	EXPERIMENTAL (WITH WIND)
10	4	5.1	6.7
12	6	8.5	12.1
14	8	16.2	21.2
16	10	21.4	24.9
19	13	31.2	32.9
23	17	43.9	38.7
27	21	52.9	47.3
37	31	67.2	59.7

The accelerated growth of the treated plants may have been related to the lower temperature of the surrounding air. After the 13th day, however, the plants in the wind lagged behind the controls. They had shorter, thinner stems and slightly narrower, shorter leaves with dry tips (fig. 1). Adverse effects of the wind treatment used were further shown by the production of fewer tillers and by less dry matter in both tops and roots. There was also a considerable decrease in the volume of the roots. Moreover, water requirement was nearly double that of the controls (table 2).

TABLE 2  
*Effects of wind upon the development of Setaria italica*  
(average of 12 plants in each lot)

CRITERIA	CONTROL (WITHOUT WIND)	EXPERIMENTAL (WITH WIND)	RATIO OF CONTROL TO EXPERIMENTAL PLANTS
Height, cm.	67.2	59.7	1:0.89
Number of tillers	5.2	4.0	1:0.77
Thickness of stalk, cm.	0.8	0.6	1:0.75
Width of widest leaf, cm.	1.44	1.27	1:0.88
Weight of shoot, gm.	4.1	2.93	1:0.71
Weight of roots, gm.	1.51	0.89	1:0.59
Volume of roots, cc.	13.75	8.5	1:0.62
Water requirement, lbs.	511.7	968.5	1:1.89
Water transpired, lbs.	6.33	8.16	1:1.29

## DISCUSSION

The depressing influence of strong wind upon the growth of vegetation is well known but quantitative data are meager. Blanchard (1934) compared the growth and yield of two orchards of Eureka lemons and found that the factor of improvement in yield due to protection from wind was 5 to 7 and in size of trees about 3. A reduction of about 50 per cent in dry weight of marigolds grown under a constant wind velocity of 15 m.p.h. was reported by Finnell (1928). Martin and Clements (1935) made a thorough study of the effect of constant wind velocities of 5, 10, and 15 m.p.h. on shoots of *Helianthus annuus*. Using different wind velocities and plants in various stages of development, they found in all experiments that leaf area, stem height and diameter, dry weight, and total transpiration, as well as number of xylem elements and xylem area, decreased with increasing wind velocity. The water requirement at the highest wind velocity, 15 m.p.h., was increased 50 per cent. These authors also give a summary of the conflicting literature on this subject, none of which makes reference to the effect upon root systems.

## SUMMARY

Plants of Italian millet (*Setaria italica* Beauv.) were grown in continuous wind 12 hours daily for 31 days. The tips and margins of the first three leaves began to dry after the fifth day. The treated plants grew more rapidly than the controls the first 13 days, but less rapidly thereafter. Tops of plants subjected to wind were shorter, lighter in weight, thinner stalked, and had narrower leaves and fewer tillers. These plants also had lighter and less bulky root systems. The water requirement was approximately doubled.

The author wishes to express his sincere appreciation to Dr. J. E. Weaver, under whose direction this work was done.

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## Studies in *Penstemon* VI. The section *Aurator*

DAVID D. KECK

*Aurator*, proposed as a new section in the scrophulariaceous genus *Penstemon*, contains eighteen species as here defined. These all occur in western North America under semi-arid conditions at moderate elevations. The plants are relatively low, herbaceous perennials, marked by their prominently glandular-viscid inflorescence, explanate anthers and usually by their prominently bearded staminode.

The following herbaria have been consulted in the course of this study:

C—University of California, Berkeley.

CAS—California Academy of Sciences, San Francisco.

CI—Carnegie Institution at Washington, Stanford University, Calif.

CM—Carnegie Museum, Pittsburgh, Pa.

F—Field Museum, Chicago.

GH—Gray Herbarium, Harvard University, Cambridge.

M—Missouri Botanical Garden, St. Louis.

Minn—University of Minnesota, Minneapolis.

NY—New York Botanical Garden.

Ph—Academy of Natural Sciences, Philadelphia.

Po—Pomona College, Claremont, Calif.

Pul—State College of Washington, Pullman.

RM—Rocky Mountain Herbarium, University of Wyoming, Laramie.

SU—Dudley Herbarium, Stanford University, Calif.

US—United States National Herbarium, Washington, D. C.

I am grateful to those in charge of these collections for permission to study materials. I am particularly indebted to Dr. F. W. Pennell, of the Academy of Natural Sciences of Philadelphia, whose authoritative suggestions on problems in *Penstemon* I have sought many times, both in regard to the present section of the genus and many others as well.

### BOUNDARIES OF THE SECTION

F. W. Pennell, in his recent monograph on the Scrophulariaceae of Eastern Temperate North America (Acad. Nat. Sci. Phila. Monogr. 1, 1–650, 1935) provisionally treated *Penstemon Cobaea* Nutt., *P. triflorus* Heller, *P. guadalupensis* Heller and *P. albidus* Nutt., as members of a distinct section, *Albidi*. To this proposal I do not agree, because the study of the four, together with the other species included in the present paper, leads me to the conclusion that all must be considered as members of a single section. Thus circumscribed, the group is natural from the standpoints of comparative morphology and distribution, and homogeneous throughout due to a

close interconnection of the components. For example, Pennell would separate the sections *Albidi* and *Cristati* on the presence of glands within the corolla-throat in the former and their absence in that position in the latter, but this criterion falters in the cases of *P. Jamesii* and *P. eriantherus*, which Pennell would assign to the *Cristati*, and in *P. guadalupensis* of his *Albidi*. *Penstemon Jamesii* is definitely glandular within the corolla in its two larger subspecies, as much so as the average species of *Albidi*. Occasionally *P. eriantherus* is moderately glandular within, especially on the lateral lobes of the lower lip. *P. guadalupensis*, on the other hand, is sometimes essentially glandless within the corolla. The four species assigned by Pennell to the *Albidi* are not villous-bearded on the lower lip of the flower, whereas the majority of the other species considered in this paper are. The lack of bearding, however, occurs in some of the latter that are otherwise notably different and widely separated geographically, so the character is one whose presence or absence runs counter to the most probable phylogenetic sequence and consequently its importance should not be magnified.

There is no geographic hiatus between the members of the *Albidi* and the *Cristati*. The various species form a network over the country, occupying adjacent areas after the manner of ecospecies that have evolved from ecotypes, and although the members of the *Albidi* are the easternmost, I find no excuse for grouping them apart, even as a subsection.

Since Pennell's treatment of these four species is adequate and generally available, I have avoided a complete repetition here, contenting myself with summarizing his distributional data and keying out his units. The latter I subscribe to fully, with the exception regarding sections, including his statement that the treatments of *P. triflorus* and *P. guadalupensis* are provisional, because my independent examination of material leads me to similar results and does not warrant additional revision. It appears to be a natural presumption that *P. guadalupensis* represents a southern derivative of *P. albidus* (or vice versa), whereas *P. Cobaea* and *P. triflorus* are most closely related to each other. Furthermore, it is to all appearances a narrow step from *P. guadalupensis*, and perhaps from *P. albidus*, to *P. Jamesii*, *P. auriberbis* and relatives.

#### Section *Aurator*, sect. nov.

Low, mostly short-lived herbaceous perennials; stems few to several crowning the taproot or praemorse rootstock, erect; leaves mostly entire but in all species at least potentially toothed, dimorphic, those of the basal rosette petiolate, the lower cauline often petiolate gradually becoming sessile upwards, the upper cauline usually widest at base and often clasping; inflorescence

± prominently glandular-pubescent; calyx-lobes lanceolate; corolla glandular-pubescent without, the throat rounded, scarcely if at all plicate, usually pilose at orifice across base of lower lip; fertile stamens glabrous, their anthers sometimes minutely ciliolate-denticulate, sterile stamen usually densely bearded with prominent flattened hairs, rarely glabrate. Type species, *P. eriantherus* Pursh. Included here are the *Albidi* and *Cristati*, variously called species-groups or sections by authors, but in compliance with Article 26 of the International Rules I am proposing a sectional name in substantive form. The Latin noun *aurator*, the gilder, is employed in reference to the prominent yellow beard found on the staminode of most species that simulates a brush dipped in gilt.

## KEY TO THE SPECIES OF SECTION AURATOR

- A. Throat glandular within but not villous; staminode lightly bearded; anther-sacs peltately explanate.
  - B. Corolla 25–50 mm. long, 9–25 mm. wide at throat.
    - C. Corolla over 35 mm. long, the throat abruptly much inflated; capsule 12–14 mm. long ..... 1. *P. Cobaea*
    - D. Corolla pale violet-purple or white; foliage pale green ..... 1a. *P. C.* subsp. *typicus*
    - DD. Corolla deep purple; foliage deeper green ..... 1b. *P. C.* subsp. *purpureus*
    - CC. Corolla less than 35 mm. long, the throat gradually and moderately inflated; capsule 11–12 mm. long ..... 2. *P. triflorus*
    - E. Cauline leaves lanceolate to ovate-oblong, usually sharply serrate; corolla mostly 30–35 mm. long, "white, pink, or pink-red" ..... 2a. *P. t.* subsp. *typicus*
    - EE. Cauline leaves widely linear to lanceolate, essentially entire; corolla mostly 25–30 mm. long, "lavender" ..... 2b. *P. t.* subsp. *integrifolius*
  - BB. Corolla 12–20 mm. long, 5–8 mm. wide at throat, white or tinged with purplish.
    - F. Leaves glabrate; corolla sparingly glandular-puberulent without and within ..... 3. *P. guadalupensis*
    - G. Corolla 15–20 mm. long; cauline leaves linear ..... 3a. *P. g.* subsp. *typicus*
    - GG. Corolla 12–15 mm. long; cauline leaves elliptic-lanceolate ..... 3b. *P. g.* subsp. *Ernesti*
    - FF. Leaves scabrid-puberulent; corolla densely glandular-pubescent without and within ..... 4. *P. albidus*
  - AA. Throat not glandular within, or if glandular, villous at orifice.
    - H. Anther-sacs dehiscent quite to proximal apices. Southern Colorado.
      - I. Corolla 18–22 mm. long, 7–8 mm. wide at throat ..... 5. *P. auriberbis*
      - II. Corolla 12 mm. long, 5 mm. wide at throat ..... 6. *P. parviflorus*
    - HH. Anther-sacs dehiscent throughout and through the partition (except in 11).
      - J. Throat viscid-glandular within (except in 7c); anther-sacs peltately explanate ..... 7. *P. Jamesii*
    - JJ. Throat not glandular within (sometimes sparingly glandular in 16).
  - K. Staminode included; ovary glabrous.
    - L. Corolla blue-purple; anther-sacs not explanate.
      - M. Inflorescence, including calyces, glandular-pubescent, not additionally puberulent. Utah-Colorado ..... 8. *P. Moffatii*
      - MM. Inflorescence, including calyces, scarcely viscid but densely puberulent.
        - N. Leaves lanceolate to elliptic, 4–8 mm. wide; staminode bearded on outer half. Utah ..... 9. *P. dotius*
        - NN. Leaves linear to linear-oblong, 2–4 mm. wide; staminode bearded throughout. Idaho ..... 10. *P. pumilus*

LL. Corolla pinkish or reddish. California.

O. Anther-sacs not explanate, 1.3 mm. long; corolla 14–20 mm. long, somewhat ventricose. East of Owens Valley.....11. *P. monoensis*

OO. Anther-sacs explanate, 0.5 mm. long; corolla 11–14 mm. long, narrowly tubular. ....12. *P. calcareus*

KK. Staminode exerted.

Q. Capsule (and ovary) glabrous.

R. Anther-sacs peltately explanate, the line of contact long; staminode densely bearded throughout with short orange-yellow hairs.

S. Corolla 13–28 mm. long. Nevada westward.....13. *P. miser*

SS. Corolla 30–35 mm. long. Utah.....14. *P. Grahamei*

RR. Anther-sacs not fully explanate, the line of contact relatively short; staminode sparingly bearded with yellow hairs.....15. *P. Gormanii*

QQ. Capsule (and ovary) glandular-puberulent.

T. Anther-sacs peltately explanate, as broad as long, the line of contact long.

U. Corolla 20–35 mm. long, 9–14 mm. wide at throat, pilose at orifice.....16. *P. eriantherus*

UU. Corolla 16–25 mm. long, 6–9 mm. wide at throat, more densely pilose at orifice.....17. *P. Cleburnei*

TT. Anther-sacs not explanate, much longer than broad, the line of contact short .....18. *P. Whitedii*

# 1. PENSTEMON COBAEA Nutt.

*Penstemon Cobaea* Nutt., Trans. Amer. Phil. Soc. 2: 5: 182, 1837.

## 1a. PENSTEMON COBAEA subsp. TYPICUS Pennell

*Penstemon Cobaea* subsp. *typicus* Pennell, Acad. Nat. Sci. Phila. Monogr.

1: 249. 1935.

*P. Hansonii* A. Nels., Univ. Wyom. Publ. Bot. 1: 129. 1926.

Open prairies from southeastern Nebraska, southward through Kansas and Oklahoma to the Coastal Plain of southeastern Texas.

## 1b. PENSTEMON COBAEA subsp. PURPUREUS Pennell

*Penstemon Cobaea* var. *purpureus* Pennell, Proc. Acad. Nat. Sci. Phila. 73: 490. 1921.

*P. Cobaea* subsp. *purpureus* Pennell, Acad. Nat. Sci. Phila. Monogr. 1: 250. 1935.

“Rocky calcareous barrens and cliffs, valley of the White River, Ozark Mountains of northern Arkansas and southern Missouri.”

## 2. PENSTEMON TRIFLORUS Heller

*Penstemon triflorus* Heller, Contr. Herb. Franklin & Marshall Coll. 1: 92. pl. 8. 1895.

A variable species much in need of intensive field study and garden experiment.

## 2a. PENSTEMON TRIFLORUS subsp. TYPICUS Pennell

*Penstemon triflorus* subsp. *typicus* Pennell, Acad. Nat. Sci. Phila. Monogr. 1: 251. 1935.



*P. Helleri* Small, Bull. Torr. Club 25: 471, 1898.

Central Texas from Nolan to Bexar and Uvalde counties.

2b. *PENSTEMON TRIFLORUS* subsp. *INTEGRIFOLIUS* Pennell

*Penstemon triflorus* subsp. *integrifolius* Pennell, l. c.

*P. triflorus* var. *integrifolius* Cory, Rhodora 38: 407. 1936.

Western Texas from the Upper Concho River southerly to Kinney County; apparently overlapping the distribution of subsp. *typicus* in the southern portion of its range and there, due to the consequent hybridization, less clearly differentiated.

3. *PENSTEMON GUADALUPENSIS* Heller

*Penstemon guadalupensis* Heller, Contr. Herb. Franklin & Marshall Coll. 1: 92. pl. 7. 1895.

I have seen very scanty material of this species and so am relying wholly upon Pennell's classification.

3a. *PENSTEMON GUADALUPENSIS* subsp. *typicus* Pennell

*Penstemon guadalupensis* subsp. *typicus* Pennell, l.c. 252.

In the upper drainages of the Colorado and Guadalupe rivers of central Texas, from Nolan and Comanche counties to Kerr County.

3b. *PENSTEMON GUADALUPENSIS* subsp. *ERNESTI* Pennell

*Penstemon guadalupensis* subsp. *Ernesti* Pennell, l.c.

*P. guadalupensis* var. *Ernesti* Cory, Rhodora 38: 407. 1936.

Valley of the upper Colorado River in western Texas.

4. *PENSTEMON ALBIDUS* Nutt.

*Penstemon teretiflorus* Nutt., Fraser's Catal. 2, n. 66, 1813, nomen nudum.

*P. albidus* Nutt., Gen. Pl. 2: 53. 1818.

*P. viscidulus* Nees, in Neuwied, Reise Nord-Amer. 2: 444. 1841.

*Chelone albida* Spreng., Syst. Veg. 2: 813. 1825.

A widespread species of the prairies and plains east of the continental divide from southern Manitoba, Saskatchewan and Alberta, southward to western Minnesota and Oklahoma, northern Texas and easternmost New Mexico.

5. *PENSTEMON AURIBERBIS* Pennell

*Penstemon auriberbis* Pennell, Contr. U.S. Nat. Herb. 20: 339. 1920.

Stems 10-20 cm. tall, pubescent; leaves linear to linear-lanceolate, 4-8 cm. long, 2-7 mm. wide, entire or nearly so, glabrous or usually puberulent; calyx-lobes linear-lanceolate, usually attenuate; corolla 18-22 mm. long, 7-8 mm. wide at throat, pale lilac to purplish blue with faint guide lines, not

glandular within, the throat ampliate, the limb spreading, the lower lip pilose at base; anther-sacs widely divaricate, dehiscent quite to proximal apices, not explanate; staminode  $\pm$  exserted, dilated apically, densely bearded for its entire length with long yellow hairs.

Valleys of the Arkansas and Rio Grande rivers in southern Colorado. Type locality: "a dry sandy sagebrush slope, east of Fountain Creek, northeast of Pueblo, Pueblo County, Colorado, altitude about 1,400 meters."

COLORADO. KIOWA Co.: 10 mi. w. of Haswell, *Ownbey* 752 (CI). EL PASO Co.: Colorado Springs (GH); 15 mi. S. of Colorado Springs, (CI); 18 mi. S. of Colorado Springs, *Keck* 870 (C, CAS, CI, M, Ph, Po, SU); Fountain (M). FREMONT Co.: Canon City, *Pennell* 6312 (F, GH, M, NY, RM, US), *Nelson* 10543 (C, M, NY, RM). PUEBLO Co.: Pueblo, *Pennell* 5731 (NY, type; isotypes GH, RM, US), 5733 (F, M, NY, Ph); Swallows, *Baker* 6 (C, GH, M, NY, RM, US). OTERO Co.: Apishipa Creek, *Osterhout* 2039 (RM); Rocky Ford, *Osterhout* 2084 (NY). HUERFANO Co.: Walsenburg, *Bethel et al.* 4284 (CAS, CI, M, Ph, RM, SU, US), *Nelson* 11523 (C, M, NY, RM, SU); La Veta (Ph); Badito, *Rydberg & Vreeland* 6610 (NY); La Veta Pass, *Bethel et al.* 4283 (NY, Ph, RM, US). ALAMOSA Co.: Alamosa, *Porter* 2029 (CI). COSTILLA Co.: Sangre de Cristo Creek, *Rydberg & Vreeland* 5635 (NY). LAS ANIMAS Co.: Trinidad, *Eastwood* 5587 (CAS); Barela (CAS, NY). NEW MEXICO. UNION Co.: Emery Gap to Branson, *Eggleston* 20150 (NY).

6. *PENSTEMON PARVIFLORUS* Pennell

*Penstemon parviflorus* Pennell, Contr. U.S. Nat. Herb. 20: 340. 1920.

Stems 15–20 cm. tall, cinereous-puberulent; leaves linear to linear-ob-lanceolate, 3–5 cm. long, 3–5 mm. wide, finely canescent, entire; calyx-lobes linear-lanceolate, 8 mm. long; corolla 12 mm. long, 5 mm. broad at throat, probably purplish blue, internally not glandular, the throat moderately ampliate, the limb spreading, the lower lip pilose at base; anther-sacs widely divaricate, dehiscent quite to proximal apices, not explanate; staminode scarcely exserted, dilated apically, densely bearded for almost its entire length with long yellow hairs.

Known only from the type collection, made at Mancos, Montezuma County, Colorado, July, 1890, by Alice Eastwood, which I have seen in the U. S. National Herbarium.

This species remains obscure. Additional collections have not been forthcoming despite the fact that much collecting has been done in Montezuma County in the years following Miss Eastwood's original collection and Pennell's description of the species. That it is a rare endemic and not a random introduction of some species from a distant area seems certain,

because its nearest known relative is the Coloradan *P. auriberbis* Pennell, a species that differs in several features.

Pennell did not note that all the upper leaves of the type specimen are ternate, while the several basal pairs are alternate. If this should prove to be a specific character, it would be a material aid in quickly identifying *P. parviflorus*, for no other species of this subgenus has ternate leaves. But as there is only one specimen preserved at present, we are unable to ascertain whether this will prove to be a constant feature of the species or a unique occurrence. If the latter proves to be the case, or if the species cannot be rediscovered, the possibility must be considered that a seed of *P. auriberbis* was accidentally distributed to Montezuma County of a genetically aberrant constitution, so that it sprouted into a plant that flowered without developing a basal rosette, and that had ternate upper leaves and flowers of less than two-thirds the normal size.

#### 7. PENSTEMON JAMESII Benth.

*Penstemon Jamesii* Benth, in DC., Prod. 10: 325. 1846.

Stems 1-4.5 dm. tall, glabrate to pubescent below, always glandular-pubescent above; leaves linear to oblanceolate, 2-10 cm. long, 2-10 mm. wide, entire or sometimes undulately serrate, glabrous or puberulent; calyx-lobes narrowly to broadly lanceolate, acuminate, entirely herbaceous or the margin narrowly scarious; corolla 18-32 mm. long, blue-lavender, the throat broadly ampliate and ventricose; upper lip projecting, glabrous within; lower lip reflexed, usually glandular-pubescent within and prominently bearded with long whitish hairs at orifice, the orifice 9-15 mm. wide, guide lines extending into throat from both lips; anther-sacs widely divaricate, explanate, *ca.* as broad as long; staminode exserted, bearded almost its entire length with long often septate yellow hairs.

Southern Utah to northern Arizona, southwestern Colorado, New Mexico and the mountains of southwestern Texas.

#### KEY TO SUBSPECIES

Lower lip glandular-pubescent within.

Corolla 25-32 mm. long, 10-15 mm. wide.....7a. *P. J.* subsp. *typicus*

Corolla 17-22 mm. long, 7-10 mm. wide.....7b. *P. J.* subsp. *ophianthus*

Lower lip glabrous within; corolla 14-16 mm. long, 5-6.5 mm. wide. .7c. *P. J.* subsp. *breviculus*

#### 7a. *Penstemon Jamesii* subsp. *typicus*, nom. nov.

*Penstemon Jamesii* Benth., l.c.

*P. similis* A. Nels., Bull. Torrey Club 25: 548, 1898. Nelson redescribed this New Mexican species under this name, believing that *P. Jamesii* was the plant of the Red Desert of southwestern Wyoming, which, instead is *P. Cleburnei* Jones. The first number he cites is *Fendler 575*, which was probably collected near Santa Fe.

Eastern New Mexico to southwestern Texas. Type locality: "in montibus Scopulosis (James in itinere Longii!)" The route followed by James' part from the Arkansas River in Colorado near the vicinity of what is now La Junta, was straight south into New Mexico veering easterly to strike the Canadian River in western Texas. Apparently the only portion of New Mexico traversed by the party lies now in Union County and we suspect the type came from there.

NEW MEXICO. Exact station unknown, Long's Expedition, *Dr. James* (NY, type). COLFAX Co.: Vermejo River, *Goodding* 18 (CI); Raton, *St. John* 72 (GH), *McKelvey* 4861 (CI); Ute Park, *Standley* 13745 (US); E. of Cimarron, *Wilkins* 2456 (Ph). MORA Co.: between Wagon Mound and Las Vegas, *McKelvey* 4909 (CI); Mora, *Arsene & Benedict* 17168 (Ph). SAN MIGUEL Co.: Pajarila (M); Las Vegas, *Arsene* 19413 (Po), *Goodding* 17 (CI); San Miguel, *Fendler* 579 (GH); Arroyo Pecos, *Standley* 5168 (US); Las Vegas to Santa Fe, *Osterhout* 7032 (Ph); Rowe, *Pringle* (F). SANTA FE Co.: Santa Fe, *Fendler* 575 (CI, F, GH, M, NY, Ph, US), *Heller* 3605 (GH, M, NY, Po, Pul, SU); Glorieta, *Vasey* (GH, US). SANDOVAL Co.: Placitas (RM); Forest Park, Sandia Mts., *Castetter* 1265 (RM); Las Palomas, Sandia Mts., *Ellis* 480 (NY). QUAY Co.: Tucumcari, *Abbott* (CM). LINCOLN Co.: Lincoln, *Earle* 653 (NY); W. of Hondo, *Wilkins* 2122 (Ph). OTERO Co.: Highrolls (CI, Ph); Nogal Canyon, Sacramento Mts. (CI). EDDY Co.: Carlsbad Caverns, *Nelson* 11408 (C, RM); Queen, *Standley* 40687 (US); Guadalupe Mts., near Three Forks of Rocky Arroyo, *Wilkins* 1855 (Ph); Last Chance Canyon, *Wilkins* 1913 (Ph). TEXAS. PARMER Co.: Farwell, *McKelvey* 2770 (Ph). CULBERSON Co.: Pine Canyon, Guadalupe Mts., *Chase* 5994 (US); Van Horn's Wells, *Thurber* 570 (NY). JEFF DAVIS Co.: Fort Davis, *Jones* 25601 (Po). BREWSTER Co.: Alpine, *Palmer* 30564 (Ph); 5 mi. W. of Alpine, *McKelvey* 1986 (Ph).

7b. *Penstemon Jamesii* subsp. *ophianthus* (Pennell), comb. nov.

*Penstemon ophianthus* Pennell, Contr. U.S. Nat. Herb. 20: 343. 1920.

*P. pilosigulatus* A. Nels., Univ. Wyom. Pub. Bot. 1: 130. 1926. "This also was secured near Flagstaff, Arizona and is reported by Mr. Hanson from 'the Canadian zone and above.' His no. 554, June 6, 1923, is the type." The type is characteristic of much material from northern Arizona which develops a compact rosette of rather short, narrow leaves from which the flowering stem, with its well spaced and linear leaves, emerges. However, gradations are numerous to forms with more ample foliage such as the type of *P. Jamesii ophianthus* has, and these obscure a true regional difference among the races of this subspecies.

Western Colorado and southern Utah southward to western New Mexico and northern Arizona. Type locality: "Thurber, Utah."

COLORADO. MONTROSE Co.: Naturita, *Payson* 347 (CM, F, GH, M, Pul, RM). UTAH. WAYNE Co.: Thurber, *Jones* 5708 (US, type; isotypes M, NY, Po); Bicknell, *Cottam* 4509 (Ph). GARFIELD Co.: *Siler* (M); Pleasant Creek Camp, *Dixon* 286 (RM). WASHINGTON Co.: Chadwick's above St. George, April 1913, *Johnson* (Po, a poor, atypical specimen, possibly distinct). NEW MEXICO. ? Co.: between Gallup and Albuquerque, *McKelvey* 2336 (GH, Ph, Po). MCKINLEY Co.: W. of Gallup, *McKelvey* 4593 (CI); Fort Defiance, *Palmer* 108 (NY). VALENCIA Co.: San Mateo, Mount Taylor, *Castetter* 1794 (RM). SANDOVAL Co.: Sandia Mts., *Ellis* 374 (NY, US). SOCORRO Co.: Santa Magdalena Mts., *Vasey* (GH, US); Magdalena, *Herrick* 652 (US). CATRON Co.: W. of Patterson, *Wooton* (US). ARIZONA. MOHAVE Co.: Sturgenegger Ranch, *Cottam et al.* 4164 (Ph). COCONINO Co.: Red Butte, *Ward* (US); El Tovar, Grand Canyon, *Eastwood* 5661 (CAS); 10 mi. S. of Grand Canyon, *Ward* (NY); Grand Canyon-Flagstaff, *Ferris & Duncan* 2281 (CAS, M, NY, SU); Williams, *Jones* (Po); San Francisco Peak, *Purpus* 7074 (C, M, Po, US); Flagstaff, *Hanson* 554 (RM, type of *P. pilosigulatus*; isotype M), *MacDougal* 130 (C, GH, NY, Ph, RM, US); 8 mi. E. of Flagstaff (CI, Ph); 15 mi. E. of Flagstaff (M, NY, Ph). YAVAPAI Co.: Ash Fork, *Jones* 94 (C, GH). NAVAJO Co.: Cedar Springs, *Toumey* 368 (SU, US); Taylor (US); Pinedale, *Zuck* (US). GREENLEE Co. (?): San Francisco Mts., July 1, 1892, *Wooton* (NY, US).

7c. *Penstemon Jamesii* subsp. *breviculus*, subsp. nov.

Corollis 14–16 mm. longis 5–6.5 mm. latis fere tubulosis haud glandulosis intus, ceteroqui subsp. typicus similibus.

Type: *Baker, Earle & Tracy* 410, collected on dry plains below Mancos, Montezuma County, Colorado, July 8, 1898, Pomona College Herbarium, number 7232. Isotypes CI, F, GH, M, NY, Ph, US.

COLORADO. MONTEZUMA Co.: E. of Cortez, *McKelvey* 4640 (CI). NEW MEXICO. SAN JUAN Co.: Aztec, *Baker* 601 (GH, M, NY, Po, RM, US); Chuska, *Marsh* 102 (US).

Possibly careful field study would demonstrate that this unit is fully deserving of specific rank. On the present data, however, it appears to compose a natural subspecies, the small, scarcely inflated corollas, without glands within the limb or throat, being a constant characteristic of the collections cited and differing appreciably from all others in the species. Pennell cited the type collection under his *P. ophianthus*, but the two do not overlap in corolla-size. It is true that the type collection of *P. ophianthus*, and *Payson* 347, from Naturita, Colorado, both from the periphery of the subspecies and not typical of the unit, have very few glands within

the lower lip; but normally *P. Jamesii* subsp. *ophianthus* is obviously glandular on the lower lip.

It became necessary to reduce *P. ophianthus* to subspecific rank after studying many collections from New Mexico, because subsp. *typicus* contains much variation even within so restricted a region as Santa Fe County. The variable characters include first of all flower-size and the amount of inflation in the throat, then leaf-shape, serration or non-serration of the margin, sepal-length, height of plant, compactness of the inflorescence, etc. There is about as much variation within neighboring races of subsp. *typicus* as between some of them and subsp. *ophianthus*. The range of *typicus* merges with that of *ophianthus* and no evident break in the morphology of the forms across an east to west transect has been discovered. Nevertheless, two excellent subspecies exist that roughly divide the bulk of the species into eastern and western halves, while subsp. *breviculus* forms a marginal island in the general distribution whose members may owe their unique character to an early contact with some other species of the section.

#### 8. *PENSTEMON MOFFATII* Eastw.

*Penstemon Moffatii* Eastw., Zoe 4: 9. 1893.

Stems 1-3 dm. tall, puberulent; leaves entire or essentially so, puberulent, basal with linear-ob lanceolate to elliptic blades, cauline linear-oblong; calyx-lobes acuminate, glandular-pubescent; corolla 12-22 mm. long, blue-purple (?), neither glandular nor pubescent within or sometimes sparingly pilose at base of lower lip; anther-sacs widely divaricate, dehiscent throughout but not explanate; staminode mostly included, moderately dilated apically, with a moderate yellow beard along its outer half.

#### KEY TO SUBSPECIES

Corolla 15-22 mm. long, throat ample.

Blades of basal leaves narrowly ovate to elliptic; upper cauline leaves  $\pm$  cordate-clasping at base..... 8a. *P. M.* subsp. *typicus*

Blades of basal leaves oblanceolate; upper cauline leaves not widest at sessile base..... 8b. *P. M.* subsp. *Paysonii*

Corolla 10-12 mm. long, very narrow; blades of basal leaves oblanceolate..... 8c. *P. M.* subsp. *Marcusii*

#### 8a. *Penstemon Moffatii* subsp. *typicus*, nom. nov.

*Penstemon Moffatii* Eastw., l.c.

Central Utah to western Colorado. Type locality: Grand Junction, Colorado.

UTAH. UTAH CO.: Thistle, *Jones* (GH, NY, SU). DUCHESNE CO.: Duchesne (Theodore), *Jones* (Po). GRAND CO.: Thompson's Springs (Thompsons), *Jones* (C, CAS, F, GH, M, NY, Po, RM, SU, US). COLO-



RADO. MESA Co.: Mack, Jones (Po); Grand Junction, May 1892, *Eastwood* (CAS, type; isotypes C, GH, M, US), May 1891, *Eastwood* (M, NY, SU), *Pennell* 6173 (F, GH, NY, RM, US), Gunnison Mesa, Grand Junction, *Eastwood* 5100 (CAS, SU); 7 mi. S.E. of Grand Junction, *Keck* 802 (CI); De Beque, *Osterhout* 4249 (Ph), 4482 (NY).

8b. *Penstemon Moffatii* subsp. *Paysonii* (Pennell), comb. nov.

*Penstemon Paysonii* Pennell, Contr. U.S. Nat. Herb. 20: 342. 1920.

Montrose County, Colorado. Type locality: Naturita.

COLORADO. MONTROSE Co.: Naturita, *Payson* 257 (M, type; isotypes F, GH, CM, Minn, RM), 990 (RM), 3864 (C, GH, M, Ph, RM).

8c. *Penstemon Moffatii* subsp. *Marcusii*, nom. nov.

*Penstemon pseudohumilis* Jones, Contr. West. Bot. 12: 65. 1908; not Rydb., Mem. N. Y. Bot. Gard. 1: 347. 1900.

Carbon County, Utah. Type locality: Price.

UTAH. CARBON Co.: Price, June 29, 1898, *Marcus E. Jones* (Po, type), June 20, 1898, *Stokes* (C).

This species has a rather discontinuous distribution over one of the less well known regions botanically. Consequently it is not easy to properly evaluate the importance of the considerable variation in flower-length that may be as great as 4 to 5 mm. from single localities such as Thompsons, Grand Junction and Naturita. Considering the high aridity of the region during much of the year, such variations may principally be due to modification alone. At all events, the local variability greatly decreases the importance of this character which was the chief one advanced in support of *Paysonii* as a species. Also, subspp. *Paysonii* and *Marcusii* are very similar in foliage characters although they are far apart geographically and a portion of the range of subsp. *typicus* intervenes between them. Such recombinations of characters speak for the phylogenetic unity of the species.

9. *PENSTEMON DOLIUS* Jones ex Pennell

*Penstemon dolius* M. E. Jones ex Pennell, Contr. U. S. Nat. Herb. 20: 341. 1920.

Stems 5-15 cm. tall, cinereous-puberulent; leaves entire, densely cinereous-puberulent throughout, basal with lanceolate to elliptic blades, upper cauline linear-lanceolate, narrowed to a petiole-like base; inflorescence scarcely viscid; calyx-lobes linear-lanceolate, acuminate, densely puberulent with a few gland-tipped hairs interspersed; corolla 15-20 mm. long, 4-6 mm. broad at throat, blue-purple, glabrous within or sometimes sparingly pilose at base of lower lip; anther-sacs widely divaricate, dehiscent throughout but not ex-

planate; staminode included, moderately dilated apically, with a sparse to moderate yellow beard along its outer half; capsule glabrous.

Upper Sonoran Zone, from 5,000 to 7,300 ft. elevation, in heavy soils from Elko County, Nevada, to Duchesne and Sevier counties, Utah. Type locality: "Willow Springs, Nevada." Personal communication from Jones locates this as Willow Springs Pass, Deep Creek Mts. (E. flank of the Ibapah Mts.), west of Troutcreek, Juab County, Utah, not far east of the Nevada state line.

NEVADA. ELKO Co.: Ferguson Spring, June 14, 1900, *Jones* (Po); Cobre, June 26, 1907, *Jones* (Po). WHITE PINE Co.: Aurum, May 30, 1893, *Jones* (Po). UTAH. TOOELE Co.: Deep Creek (=Ibapah, acc. M.E.J.), June 6, 1891, *Jones* (Po), June 3, 1917, *Jones* (Po); Clifton, June 19, 1891, *Jones* (Po). JUAB Co.: Willow Spring Pass, June 5, 1891, *Jones* (US, type; isotypes C, CAS, CI, GH, M, NY, Po). SEVIER Co.: 3 mi. N. of Redmond, *Eggleston 11130* (US); Vermilion, June 4, 1901, *Jones* (Po). DUCHESNE Co.: Duchesne (Theodore), May 12, 1908, *Jones* (Po), May 14, 1908, *Jones* (Po); Duchesne (Theodore) to Myton, May 19, 1908, *Jones* (CI, M, NY, Po, SU, US).

#### 10. *PENSTEMON PUMILUS* Nuttall

*Penstemon pumilus* Nutt., Jour. Acad. Phila. 7: 46. 1834.

Stems several from the branching root-crown surmounting a praemorse rootstock, 5-12 cm. tall, cinereous-pubescent throughout; leaves linear to linear-oblongate or narrowly spatulate, 15-25 mm. long, 2-5 mm. wide, obtuse or acute, entire, all narrowed to base; inflorescence scarcely viscid, abbreviated; calyx 6-7 mm. high, the lobes acuminate, puberulent with fine gland-tipped hairs interspersed; corolla 14-20 mm. long, 4-6 mm. broad at throat, blue-violet, sparingly glandular-puberulent without, glabrous within; anther-sacs divaricate, dehiscent throughout but not explanate; staminode included, with moderate beard of short yellow hairs almost throughout its length.

Infrequent in the valleys of the upper Salmon and Little Lost rivers, Idaho, at 1500-1900 m. elevation. Type: "On the borders of Little Goddin river, near the sources of the Columbia river. Flowering in June." Wyeth knew the Little Lost River as the Little Goddin River.

IDAHO. CUSTER Co.: 7 mi. up Morgan Creek, *Pennell 15274* (CI, Ph); Challis, *Macbride & Payson 3211* (GH, M, RM). BUTTE Co.: Little Goddin River (Little Lost River), *Wyeth* (British Museum, type, the label bearing the additional information "dry soil nr. a brook"; phototypes C, CI, GH, SU; isotypes GH, NY, Ph); 3 mi. N. of Howe, *Pennell 15190* (CI, Ph); 5 mi. NW. of Howe, *Pennell 15195* (CI, Ph).

The type collection is the only one I have seen in good flower. However,

old flowers on the two collections from Custer County appear to have been no longer than 10–14 mm., whereas those on the type range in length from 16–20 mm. Inadequate material at present prevents me from stating whether this species is variable in flower-size merely at random or in definite geographic directions.

*Penstemon pumilus* grows in the same region with *P. Whitedii* subsp. *tristis*, but is readily distinguishable by its glabrous capsule, sparingly bearded staminode, small less divergent anther-cells, canescent herbage, and by its finer, shorter, gland-tipped hairs on the calyx.

The closely allied *P. dolius* of Utah and eastern Nevada is separable from *P. pumilus* by its broader leaves and its longer and narrower sepals, but the two apparently are of common origin.

#### 11. PENSTEMON MONOENSIS Heller

*Penstemon monoensis* Heller, *Muhlenbergia* 2: 246. 1906.

*P. divergens* Jones, *Contr. West. Bot.* 12: 64, 1908. Type locality: "Bishop, Owen's Valley, California, 5000 feet altitude, May 15, 1897 [M. E. Jones]."

Stems 15–35 cm. tall, densely cinereous-puberulent; leaves entire, the margin often crisped, densely scurfy puberulent, large, the basal with lance-oblong to broadly oval blades, the cauline narrowly elliptic below to deltoid-ovate and broadly clasping above; calyx-lobes acuminate, viscid-pubescent; corolla 14–18 or 20 mm. long, 4–6 mm. broad at throat, "rose-purple" or "wine-red," not marked with guide lines, glabrous and glandless within or sometimes sparingly pilose at base of lower lip; anther-sacs divergent, dehiscent quite to proximal apices, not explanate; staminode not reaching to orifice, not dilated, strongly bearded for its outer half with fine rather short yellow hairs; capsule glabrous.

Occasional on the desert ranges bordering Owens Valley, California, at elevations of 1400–1600 meters. Type locality: "The type is no. 8331 [Heller], collected May 25, 1906, in the extreme southern part of Mono County, California, along the base of the White Mountains near the Southern Belle Mine."

CALIFORNIA. MONO Co.: Coldwater Canyon, White Mts., May 1913, *K. Brandegee* (C); near Southern Belle Mine (Inyo Co.), *Heller* 8331 (C, F, GH, M, NY, Ph, SU, US, isotypes). INYO Co.: Bishop, May 15, 1897, *Jones* (Po, type of *P. divergens*; isotypes C, M, US); Lee Mine, Hunter Ranch Mts., *Austin* 526 (C, NY); 15 mi. N. of Darwin, *Hall & Chandler* 7176 (C, GH, Po, SU); 2 mi. W. of Darwin, *Munz* 12490 (C, F, M, Po, SU); Darwin, *Hall & Chandler* 7104 (C, M).

#### 12. PENSTEMON CALCAREUS Brandegee

*Penstemon calcareus* Brandegee, *Zoe* 5: 152. 1903; not Jones, 1908.

*P. desertorum* Jones, Contr. West. Bot. 12: 59. 1908. Type locality: "This grows in clefts of the rocks, at 4000 feet altitude, in the Tropical Life Zone at Kelso, California, May 2, 1906 [Jones]." This is on the west slope of the Providence Mountains. Cf. Munz & Johnston, Bull. Torrey Club 49: 42. 1922.

Stems 5–25 cm tall, densely pruinose-puberulent, anthocyanous; leaves entire or some of them remotely and obscurely denticulate, densely puberulent on both surfaces to glabrate on the lower side, basal with elliptic to broadly ovate blades 15–40 mm long, cauline linear- to oblong-lanceolate, those subtending the inflorescence often subcordate-amplexicaul; calyx-lobes anthocyanous, narrowly lanceolate, viscid-pilose, accrescent; corolla 12–17 mm long, 2.5–4 mm broad at throat, light rose-red to rose-purple, not marked with guide lines nor glandular within, sparingly pilose at base of lower lip, the limb equally 5-lobed; stamens short; anther-sacs widely divaricate, very small, almost as broad as long, explanate; staminode included, not dilated, strongly bearded for  $\frac{2}{3}$  its length with rather coarse golden-yellow hairs; capsule glabrous.

Localized in the Grapevine Mountains, at the north end of Death Valley, and in the Providence Mountains, Mohave Desert, California, at elevations of 1200–1800 meters. Type locality: "... the face of perpendicular limestone cliffs of Providence Mt."

CALIFORNIA. Inyo Co.: Titus Canyon, Grapevine Mts., May 31, 1935, *Gilman* (Po); Leadfield, Grapevine Mts., 5000 ft., *Gilman* 2361 (Po), ditto, 6000 ft., *Gilman* 2384 (CI, Po), ditto, 1109 (US). San Bernardino CO.: Providence Mts., May 27, 1902, *T. S. Brandegee* (C, type; isotype C); Bonanza King Mine, *Munz, Johnston & Harwood* 4154 (Po, RM, SU, US); Kelso, May 2, 1906, *Jones* (Po, type of *P. desertorum*; isotypes C, Ph).

The desert mountain ranges in which this species has been found are about 160 miles apart and it might be wondered that a species of so limited a distribution, so ruthless an environment and so little opportunity for migration had not produced a recognizably distinct race at each center of its distribution. As a matter of fact, the first collection that came to my notice from the Grapevine Mts., namely the Titus Canyon specimen, differed from the Providence material in having greener leaves, narrower corollas, longer stamens, anther-cells of different shape and a hooked staminode with shorter beard. Subsequent collections from the Grapevines, however, have minimized or reversed these differences with the exception that in all, the leaves have less puberulence and the staminode has a shorter beard. It is well known that the desert environment may effect wide modifications in the same plant from one season to the next. In this species, as yet relatively poorly collected and in which considerable variability has been noted to occur in the floral structures at one locality, there can be but

little justification at present for stressing the minor morphological differences that happen to coincide with the geographical.

The discovery of *P. calcareus* in the Grapevine Mts. brings its known range much closer to that of *P. monoensis*, the other reddish flowered Californian member of this section. The two species share many features in common and are surely very closely related, but a number of qualitative differences separate them. *Penstemon monoensis* has a larger and somewhat ventricose corolla, minutely denticulate-ciliate anther-cells that are not explanate and of more than twice the length, and a more densely and softly bearded staminode.

### 13. PENSTEMON MISER A. Gray

*Penstemon miser* A. Gray, Syn. Fl. 2(1): 441. 1886.

Stems 10–25 cm tall, cinereous-puberulent; leaves mostly entire, some remotely serrulate or sinuately toothed, densely cinereous-puberulent throughout, basal with linear-lanceolate to elliptic blades, upper cauline linear to oblong; calyx-lobes acuminate, strongly glandular-pubescent, not puberulent, variable in size; corolla markedly variable, 13–28 mm long, 4.5–10 mm wide (!), dull lavender, purple guide lines within throat, not glandular within, strongly pilose with yellow-white hairs at base of lower lip; anther-sacs widely divaricate, very small, as broad as long, explanate or nearly so; staminode exerted, not dilated, strongly bearded for its entire length with stiffish deep orange hairs; capsule glabrous.

Malheur County, Oregon, southward to central Nevada and northeastern California, at elevations of 900 to 2200 meters. Type locality: "Eastern Oregon, along the Malheur River, *Cusick*."

OREGON. MALHEUR CO.: sterile soils of the Malheur (River), *Cusick* 1239 (GH, type; isotypes Ph, US); Malheur Valley near Harper Ranch, *Leiberg* 2226 (C, GH, NY, US). HARNEY CO.: East base of Stein's Mt., May 30, *Train* (Oberlin). CALIFORNIA. Modoc Co.: 9 mi. W. of Alturas, near Pitt River, *Applegate* 869 (SU, US). LASSEN CO.: top of Diamond Mt., Susanville, Perkin's Ranch, June 28, 1897, *Jones* (Po). NEVADA. ELKO CO.: E. of Wells, *Eastwood & Howell* 317 (CAS, CI); 8 mi. S. of Wells, *Keck* 921 (CI, SU); Sprucemont, July 21, 1891, *Jones* (Po); Overland Pass, Ruby Mts., *Mason* 4823 (CI). WHITE PINE CO.: 7 mi. S.W. of Ely, *Keck* 616 (CI, SU). NYE CO.: 4.8 mi. E. of Currant at White Pine County line, *Keck* 605 (C, CAS, CI, GH, M, NY, Ph, Po, Pul, SU, US); S. Twin River, June 8, 1933, *Goddard* (C, CI). EUREKA CO.: Eureka, *Kennedy* 845 (RM); Robert's Station, Monitor Valley, *Watson* 778 (GH, NY, US).

The variability in flower-size in *P. miser* is perplexing. Material from

Malheur Co., Oregon, is relatively small-flowered (15 mm. long, 5–6 mm. wide), with a gradually ampliate but narrow throat; that from Harney Co. is appreciably larger in this respect, while in that from Modoc Co., California, it is half again as long and 9 mm. wide, the ampliate throat flaring abruptly from the narrow tube. In eastern Nevada the situation is repeated with even more variation. In Elko Co. the collections tend to be rather uniformly larger than the type and more ampliate, but less abruptly ventricose than the Applegate collection from Modoc County. *Keck 605* and *616* are similar with corollas 13–14 mm. long and only 4.5 mm. wide. In startling contrast is the collection from relatively nearby in Nye County, *Goddard*, in which the flowers are 28 mm. or more long and 10 mm. wide! It is determined from an ample number of collections that differences in flower-size run counter to geographic divisions, so we cannot do otherwise on the basis of present evidence than admit these striking variations within the same taxonomic unit. The only other character that is noticeably variable is the shape of basal leaves, which may be nearly linear or almost oval in the same local colony. In other respects this species is quite uniform and there is no indication that it is unnatural.

14. *PENSTEMON GRAHAMII* Keck

*Penstemon Grahamii* Keck ap. Graham, *Annals Carnegie Mus.* 26: 331. 1937.

Stems few (1–3), erect, from a praemorse fibrous-rooted rootstock, 12–18 cm tall, retrorse-pubescent quite to the base; leaves entire, rarely obscurely toothed, glabrous below the inflorescence or essentially so, coriaceous, prominently reticulate veined, slightly glaucous, dimorphic; basal with lance-ovate to oval blade, the largest of which are 20–35 mm long, 15–20 mm wide, obtuse, with winged petioles half as long; cauline oblong, clasping or subcordate at base, obtuse or acute, very gradually reduced within the inflorescence, the lower pairs  $\pm$  equaling the flowers; inflorescence glandular-pubescent, composed of 2–6 verticillasters; peduncles nearly erect, stout, 3–5-flowered; calyx 7–9 mm high, accrescent, moderately pubescent with prominent gland-tipped hairs, the lobes lanceolate, merely acute,  $\pm$  coriaceous, the margin at base narrowly hyaline; corolla 30–35 mm long, 11–12 mm broad at throat, light to deep lavender, lower lip striped with red-purple, glandular-pubescent without, glabrous within except for a sparse beard of white villous hairs across the base of lobes of lower lip; tube narrow, abruptly expanding into a strongly arched throat not as long; limb equaling or exceeding throat, widely gaping, the erect upper lip 10–12 mm long, its lobes  $\frac{1}{3}$  the length, exceeding the sharply recurved lobes of the lower lip; anthers exceeding orifice, the sacs widely divaricate, explanate, almost as broad as long; staminode exerted, prominently and densely bearded on all sides for its entire length with deep orange flattened hairs 0.5 mm long, not dilated but falcate apically; ovary and capsule glabrous.



Type: Edward H. Graham, no. 7883, Carnegie Museum Herbarium, collected on a talus slope, west side of Green River, south of mouth of Sand Wash, Uintah County, Utah, at 1370 meters altitude, May 27, 1933.

Known from one other collection taken on a bench west of Green River, north of the mouth of Sand Wash, Uintah County, Utah, at the same elevation and date as the type, *Graham 7916* (CM, CI, Ph).

This plant is undoubtedly a very narrow endemic of the Uinta Basin. Not far to the west occurs *P. dolius*, a species with which the present novelty has very little in common; and to the southward is found *P. Moffatii*, likewise but distantly related. It has some habital features in common with *P. Cleburnei*, and a flower-size resemblance with *P. eriantherus*, both of which occur well to the northward of it in Wyoming. However, the most distinctive features of *P. Grahamii*, its corolla with peculiar shape and ratio between length of tube and throat, and its staminode, are duplicated only in *P. miser*, which occurs from Nevada westward. The remarkable flower of *P. Grahamii* is found on a smaller scale in the large-flowered forms of *P. miser*, but not elsewhere in this section. Likewise, the falcate staminode, so densely bearded throughout its length with bright orange short hairs, is quite alike in the two species except that in *P. Grahamii* the beard is quite as dense on the lower as on the upper side. Accordingly, in floral characters there is considerable similarity between *P. Grahamii* and *P. miser*, and in vegetative characters, between it and *P. Cleburnei*.

#### 15. PENSTEMON GORMANII Greene

*Penstemon Gormanii* Greene, Ottawa Naturalist 16: 39. 1902.

Stems 1-3 dm tall, glabrous below, glandular-pubescent above; leaves entire or sometimes shallowly serrulate apically, basal with narrowly oblanceolate to spatulate blades, acute or obtuse, glabrous, upper cauline lanceolate, those within the inflorescence glandular-pubescent; calyx-lobes acuminate, pilose with gland-tipped hairs; corolla 18-25 mm long, 8-10 mm broad at throat, blue-purple, not glandular within, rather strongly pilose at base of lower lip; anther-sacs widely divaricate, dehiscent throughout but not explanate, longer than broad; staminode slightly exserted, moderately bearded for more than half its length with long yellow hairs; capsule (and ovary) glabrous.

Gravelly or rocky slopes and hillsides in the drainage of the upper Yukon River and Yukon Valley, Yukon Territory and adjacent Alaska. Type locality: "Dry gravelly slopes of hills in Yukon Valley, June 9, 1899. M. W. Gorman."

ALASKA. Chandalar River, approx. 67° N. × 147° W., June 1927,

*Mertie* (F). YUKON TERRITORY. Dry Gulch, Yukon Valley, *Gorman* 1011 (US, type; isotype NY); Fifty Mile River, June 28, 1899, *Bolton* (Ph, US); Dawson, *Anderson* 1898 (NY), 1916, *Kusche* (GH), *Beauchamp Expedition* 82 (C), *Eastwood* 284 (CAS, GH, Po); banks of Klondyke, Aug. 1898–1901, *MacLean* (C, GH, Po); Five Finger Rapids, Aug. 21, 1899, *Williams* (NY), *Tarleton* 50b (NY); Lake Laberge, *Tarleton* 50a (NY); White Horse Rapids, July 13, 1930, *Setchell & Parks* (C, CAS); Carcross, *Eastwood* 690 (GH); Bear Creek, Lake Dezadeash, Aug. 6, 1920, *Müller* (Ph); Lake Noris (?), near head of Yukon River, *Schwalka* 66 (GH).

16. *PENSTEMON ERIANTHERUS* Pursh

*Penstemon eriantherus* Pursh, Fl. Am. Sept. 2: 737. 1814.

*P. cristatus* Nutt., Gen. Pl. 2: 52. 1818. Type locality: Missouri River, in the present state of South Dakota.

*Chelone erianthera* Steud., Nom. Bot. 186. 1820–4.

*C. cristata* Spreng., Syst. Veg. 2: 813. 1825.

*Penstemon saliens* Rydb., Mem. N. Y. Bot. Gard. 1: 344. 1900. Type locality: Columbia Falls, Montana.

*P. eriantherus* subsp. *saliens* Pennell, Contr. U.S. Nat. Herb. 20: 343. 1920.

Stems 1–3 dm tall, villous to canescent; leaves entire to saliently and remotely toothed, glandular-pubescent to canescent, basal with lanceolate to ovate blades, upper cauline lanceolate to oblong; calyx-lobes acuminate, strongly viscid-pubescent; corolla 20–35 mm long, 9–14 mm broad at throat, “light blue-magenta” or “purplish violet,” guide lines of deeper color within throat, not glandular within, or somewhat glandular-pubescent on particularly the lateral lobes of lower lip, strongly pilose at base of lower lip; anthers widely divaricate, explanate or nearly so, as long as wide or somewhat longer than wide, with broad line of contact; stamens prominently exserted, strongly bearded throughout its length with long yellow septate hairs; capsule (and ovary) glandular-puberulent.

Western North Dakota, South Dakota and Nebraska, westward throughout Montana and all but southwestern Wyoming to Spokane Co., Washington, avoiding Idaho by way of southern Alberta and British Columbia. Type locality: “In upper Louisiana, Bradbury . . .” According to Pennell, this was taken along the Missouri River in the present state of South Dakota.

This species has been mapped and citations made of its distribution by Pennell,<sup>1</sup> so I am confining citations here to a list of counties from which I have seen material, with full citation in the northwestern portion of the range that Pennell did not treat.

<sup>1</sup> Pennell, F. W.: Monograph I. Acad. Nat. Sci. Phila. 256. 1935, as *P. cristatus*.

NORTH DAKOTA: Mercer, Morton, Grant, Stark, Billings, Slope. SOUTH DAKOTA: Campbell, Hughes, Stanley, Mellette, Corson, Meade, Butte, Pennington, Custer. NEBRASKA: Thomas, Dawes, Morrill, Sioux. COLORADO: Weld. WYOMING: Weston, Niobrara, Goshen, Laramie, Converse, Albany, Carbon, Sheridan, Big Horn, Park, Yellowstone Nat'l Park. MONTANA: Dawson, Judith Basin, Carbon, Stillwater, Sweet Grass, Cascade, Meagher, Park, Gallatin, Lewis and Clark, Jefferson, Madison; GLACIER Co.: Midvale, *Umbach* 140 (F, NY, SU, US). POWELL Co.: Deer Lodge Valley, 1906, *Jones* (Po). DEERLODGE Co.: Anaconda, 1905, *Jones* (Po). BEAVERHEAD Co.: Lima, 1908, *Jones* (Po); Monida, 1908, *Jones* (Po). FLATHEAD Co.: Columbia Falls, *Kennedy* 53 (NY, type of *P. saliens*), *Williams* 126 (US); Kalispell, *Wilcox* 369 (NY). MISSOULA Co.: Missoula, *Kirkwood* 1390 (C, CAS, CI, F, Ph). LINCOLN Co.: Tobacco Mts., *Butler* 5043 (NY). ALBERTA: Macleod, 1913, *Moodie* (US); Crows Nest District, Castle River Forest Station, *Brinkman* 3087 (NY). BRITISH COLUMBIA: Fort Steele, *Anderson* 6245 (NY, Pul); Fairmont Hot Springs, *Sanson* 1009 (NY); Cranbrook, 1915, *Garrett* (NY). WASHINGTON: SPOKANE Co.: Spokane Falls, *Leiberg* 28 (GH); Spokane, *Kilburge* 873 (CI); between Spokane and Marshall, *Suksdorf* 9009b (Ph); Waikiki, 1913, *Turesson* (RM).

A species of so wide a distribution not unnaturally displays considerable variation. This affects many of the prominent characters including size of the plant as a whole and of its various parts individually, pubescence, leaf-shape, flower-color, bearding within the corolla, degree of explanation in the anther-cells and their shape, etc. Were two or more of these variables to become fixed over a portion of the range of *P. eriantherus*, thereby establishing a recognizable geographic unit, it would be desirable to name such a unit.

As this goes to press I learn that careful field studies during the past summer by Dr. F. W. Pennell have disclosed the occurrence of two races in western Montana that differ appreciably from each other and that stand out from other forms in this variable species because each occurs over a considerable area to the exclusion of other races.

In the vicinity of Bozeman, many collections were made of a race in which the flowers attain maximum size for the species. Apparently most, if not all, of the material from Gallatin County is assignable to this unit. It may be designated var. **grandis** Pennell et Keck, var. nov., foliis caulinis usque ad 70 mm. longis, 12 mm. latis; corolla 30-42 mm. longa latissime campanulato-ampliata. Type: *F. W. Pennell & F. B. Cotner* 20511 (Ph), from black soil over limestone, 5800-6000 ft. alt., divide between Rocky and Bridger Mts., east of Bozeman.

In Beaverhead County, a low, small-flowered form with narrowly linear cauline leaves occurs exclusively. This is var. *redactus* Pennell et Keck, var. nov., foliis caulinis usque ad 65 mm. longis 6 mm. latis; corolla 18–24 mm. longa, ore hiante. Type: *F. W. Pennell 20605* (Ph), from gravelly and stony slopes, 7100–7200 ft. alt., south-east of Sawyer, along Bear Creek, Beaverhead Mts., 16 miles east of Monida, June 28, 1937. Pennell also collected this at Lima and the material cited above from Beaverhead County is also assignable to this variety.

The type of *P. saliens* Rydb. is a specimen with unusual leaf-shape and tooting not shared by other collections from that region. To attempt to expand that concept to include all materials from western Montana northwestward leads into serious difficulties, for one must depend upon leaf characters in some cases, on flower-size in others and purely on geographic location elsewhere as, for instance, in Missoula Co., Montana. Thus, I believe that for practical considerations this species must be treated rather broadly. Sufficient detail must still be observed to satisfactorily separate *P. Whitedii* and its subspecies from *P. eriantherus*, but there the line seems to mark closely related ecospecies.

#### 17. *PENSTEMON CLEBURNEI* Jones

*Penstemon Cleburnei* M. E. Jones, Contr. West. Bot. 12: 62. 1908.

*P. auricomus* A. Nels. ex Rydb., Bull. Torrey Club 36: 688. 1909. "*Penstemon Jamesii* A. Nelson, Bull. Torrey Club 25: 547. 1898" (as to description). Type locality: Red Desert of Wyoming.

Stems 1–2 dm tall, pubescent; leaves entire, rarely obsoletely toothed, strigillose, basal with oblanceolate to broadly ovate (up to 4 cm broad) blades, upper cauline linear-oblanceolate to broadly oblong, usually obtuse; calyx-lobes acuminate, viscid-pubescent; corolla 16–25 mm long, 6–9 mm broad at throat, "purple," narrow guide lines at orifice, not glandular within, exceedingly pilose at base of lower lip; anther-sacs widely divaricate, explanate, *ca.* as long as broad, with broad line of contact, staminode slightly exserted, strongly bearded throughout its length with long golden yellow septate hairs; capsule (and ovary) glandular-puberulent.

Red Desert of southwestern Wyoming and to the base of the Uinta Mts. in adjacent Utah. Type locality: "This is common on the Green River Desert, Wyoming, at Granger and Green River, and appears to have been first collected since the time of Nuttall by Cleburne, June 27, 1875. It is also A. Nelson's no. 4716."

WYOMING. CARBON Co.: Hanna, *Payson 1691* (CAS, GH, M, NY, Ph, RM); Ft. Steele, *Nelson 5384* (C, RM); Rawlins, *Keck 915* (CI). FREMONT Co.: 8 mi. W. of Wind River, *Costello & Rawlins 2064* (CI). SWEETWATER Co.: Green River, June 27, 1875, *Cleburne* (Po, type), *Nelson*

3052 (RM, type of *P. auricomus*; isotypes GH, M, NY), Nelson 4716 (CM, F, NY, Po, Pul, RM); 21 mi. W. of Green River, Payson & Armstrong 3204 (GH, M, Ph, Po, RM); Granger, June 24, 1896, Jones (Po); Burned Fork, Williams 406 (CAS, NY, RM, Utah). UTAH. DAGGETT Co.: S. of Manila, Williams 443 (NY).

This species is closely allied with *P. eriantherus* Pursh, the two having many characters in common. The two are separable by the smaller corolla with contracted orifice, more densely pilose lower lip, and shorter, stiffer beard of the staminode in *P. Cleburnei*. This species, for the most part, is lower in stature and has broader rosette leaves than *P. eriantherus*, giving it a somewhat different aspect.

The two species occupy different geographical areas, but in Carbon County, Wyoming, they occur together and there the flowers of *P. Cleburnei* are larger than average. Also, in Big Horn County, Wyoming, a race of *P. eriantherus* is found that simulates *P. Cleburnei* in stature and flower-size, but in it the throat is broader and the staminode longer-bearded. Representative of this race are: 10-15 mi. E. of Kane, Williams 3012 (CI); near summit of Big Horn Mts., Ownbey 833 (CI); Trappen Creek, on road from Shell, Finley 25 (RM).

#### 18. PENSTEMON WHITEDII Piper

*Penstemon Whitedii* Piper, Bot. Gaz. 22: 490. 1896.

Stems 1-3 or 4 dm tall, pubescent to glabrate; leaves entire to sharply toothed, glabrous to densely cinereous-puberulent, broadly linear to lanceolate or oblanceolate; calyx-lobes acute to acuminate, strongly viscid-pubescent, not additionally puberulent; corolla 18-23 mm long, 6-9 mm wide at throat, mauve to deep red-purple throughout or the lobes more indigo, guide lines of darker color within throat, not glandular within,  $\pm$  pilose at base of lower lip; anther-sacs widely divaricate, much longer than broad, not explanate, with short line of contact; staminode scarcely exerted, usually bearded with golden yellow hairs; capsule (and ovary) glandular-puberulent.

Central Washington, northeastern Oregon, and central Idaho.

#### KEY TO SUBSPECIES

- Staminode densely bearded for almost its entire length with hairs much longer than its width.  
 Upper cauline leaves cordate-clasping at base, mostly 3 to 4 times longer than broad; verticillasters in flower 4.5-6 cm broad. .... 18a. *P. W.* subsp. *typicus*  
 Upper cauline leaves merely sessile or even narrowed at base, mostly 5 to 8 times longer than broad; verticillasters in flower 2-4 cm broad. .... 18b. *P. W.* subsp. *tristis*  
 Staminode sparsely bearded with hairs *ca.* equaling its width to glabrate or rarely glabrous. ... 18c. *P. W.* subsp. *dayanus*

#### 18a. *Penstemon Whitedii* subsp. *typicus*, nom. nov.

*Penstemon Whitedii* Piper, l.c.

*P. eriantherus* var. *Whitedii* A. Nels., Bot. Gaz. 54: 148. 1912.



Known only from southern Chelan County, Washington. Type locality: "Collected in rocky soil near Wenatchee, Kittitas county [now Chelan County], July 7, 1896. *Kirk Whited* no. 131."

WASHINGTON. CHELAN Co.: Wenatchee, *Whited* 131 (US, type; isotype Pul), 1068 (GH, US), 1102 (NY, US), 1166 (US), 1257 (US); lower Blewett Pass, *Thompson* 8307 (C, CI, M, NY, Ph, SU).

18b. *Penstemon Whitedii* subsp. *tristis* Pennell et Keck, subsp. nov.

Caulibus spithameis, foliis glaucescentibus angustis, supremis lanceolatis sessilibus, inflorescentia brevi plus minusve cum glandulis roridis, floribus et capsulis in eadem cyma accrescentibus, corolla purpurascens a basi labio infero villosissima, filamento sterili hinc longe denseque barbato.

Type: *F. W. Pennell* no. 15200, collected on a rocky calcareous mountain along Antelope Creek, Custer County, Idaho, at 1890 meters elevation, June 21, 1931, Academy of Natural Sciences of Philadelphia. Isotype CI.

IDAHO. LEMHI Co.: Salmon, *Payson* 1838 (CAS, GH, M, NY, RM), 1787 (M, RM); Salmon River, 23 mi. above Salmon, *Pennell* 15232 (CI, Ph). CUSTER Co.: Clayton, *Macbride & Payson* 3363 (GH, RM); Mackay, *Nelson & Macbride* 1421 (GH, M, F, RM), 1562 (RM); Morgan Creek, *Pennell* 15246 (CI, Ph). BLAINE Co.: Lost River Mts., near Clyde, *Macbride & Payson* 3133 (GH, RM). OREGON. WALLOWA Co.: Imnaha (River), *Cusick* 1435 (GH, Ph), *Sherwood* 133 (F).

18c. *Penstemon Whitedii* subsp. *dayanus* (Howell), comb. nov.

*Penstemon dayanus* Howell, Fl. N. W. Am. 1: 511. 1901.

*P. eriantherus* var. *argillosus* M. E. Jones, Contr. West. Bot. 12: 62. 1908. "John Day Valley, Oregon, June 6, 1902, Cusick, No. 2803." Exactly the same form that Howell had previously described.

North-central Oregon, on open dry hillsides in the drainage of the John Day and Deschutes rivers, at elevations of 300 to 1100 meters. Type locality: "Hillsides and plains, Muddy Station, John Day Valley, Oregon."

OREGON. GILLIAM Co.: Pine Creek, *Leiberg* 179 (GH, NY, Ph, Po, RM, US). ? Co.: Muddy Station, John Day Valley, May 12, 1885, *Howell* (UOregon, type; isotype GH), the same, May 11, 1885 (Ph, Pul, US); John Day Valley, *Cusick* 2803 (Po, type of *P. eriantherus* var. *argillosus*; isotypes C, CI, F, GH, NY, Ph, Pul, Minn, US). WHEELER Co.: 5 mi. N. of Mitchell, *Peck* 10091 (F, NY); 4 mi. E. of Mitchell, *Keck & Clausen* 3669 (C, CAS, CI, GH, NY, Ph, Po, Pul, SU). CROOK Co.: Crooked River, *Cusick* 1672 (C, F, M, US).

The situation in this species is somewhat unusual in that one discerns



here three geographic centers, not very closely approaching each other, and in each of which a recognizable morphological unit has appeared. These I am calling subspecies because in most respects they share common characters that strongly indicate their monophyletic origin and a continuous series of morphological variants links all the forms together. That this continuous chain of forms is geographically divisible into three parts may perhaps either be accounted for by the geological history of the region or by the comparatively modern transplantation of portions of the species into new regions. For instance, subsp. *typicus* appears to have a very restricted range in Chelan County, central Washington. Probably as a consequence, this unit is but little variable. On the other hand, it is very difficult to separate from certain forms of subsp. *tristis*, which occur no closer than the Imnaha River of northeastern Oregon. Furthermore, subspp. *tristis* and *dayanus*, which have more extensive ranges, are appreciably variable and it is this variability which ties the units together. In other words, here appear to be three elements that now possess apparent geographic isolation, but that seemingly lack a comparable structural distinctness.

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## INDEX TO AMERICAN BOTANICAL LITERATURE 1934-1937

The aim of this Index is to include all current botanical literature written by Americans, published in America, or based upon American material; the word America being used in the broadest sense.

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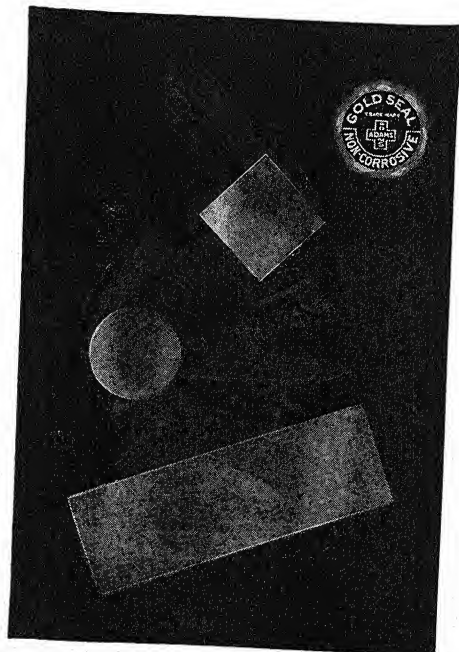
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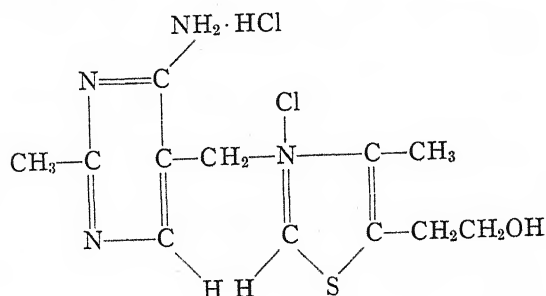
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## Thiamin and growth of species of *Phytophthora*<sup>1</sup>

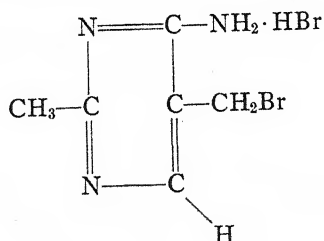
WILLIAM J. ROBBINS  
(WITH TWO FIGURES)

Since the demonstration of the necessity of thiamin (vitamin B<sub>1</sub>) for the growth of *Phycomyces Blakesleanus* by Schopfer (11) the relation of this vitamin and its pyrimidine and thiazole intermediates to the growth of a number of fungi has been reported. Thiamin hydrochloride has the following structure:

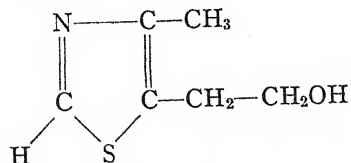


It was synthesized by Williams and Cline (15) from a pyrimidine and a thiazole of the following composition:

2-methyl-5-bromomethyl-6-aminopyrimidine hydrobromide



4-methyl-5  $\beta$  hydroxyethylthiazole



<sup>1</sup> The author gratefully acknowledges the assistance of Frederick Kavanagh and Frederick C. Robbins.

[THE BULLETIN FOR APRIL (65: 211-265) WAS ISSUED APRIL 1, 1938]

It was found that *Phycomyces Blakesleeanus* grows satisfactorily in a medium containing the two intermediates instead of the vitamin (7, 12, 13) and that the growth of *Phycomyces* is not, therefore, conclusive evidence of the presence of thiamin. In fact, it appears that *Phycomyces* actually requires thiamin and though capable of forming it from the two intermediates, it is unable to synthesize either intermediate from the mineral salts, sugar and asparagine which constitute the basic medium (7). Other fungi which grow poorly or not at all on a medium of mineral salts, sugar and asparagine are able to synthesize the vitamin thiazole but little or none of the intermediate pyrimidine (8). These organisms require for growth an external supply of the pyrimidine. Still others synthesize pyrimidine but little or no thiazole and require the latter compound (6). None of these organisms can be said to require an external supply of thiamin since they grow satisfactorily if furnished with one or both of the intermediates.

Are there fungi which require an external supply of thiamin and are incapable of using the intermediates? From our investigations we have concluded that several species of *Phytophthora*, probably most of this genus belong to such a group (9).

#### METHODS AND MATERIALS

The following species of *Phytophthora* kindly furnished by C. M. Tucker were used:

*Phytophthora Boehmeriae* Saw., *P. cactorum* (L. and C.) Schwet., *P. cambivora* (Petri) Buis., *P. capsici* Leon., *P. cinnamomi* Rands, *P. citrophthora* (Sm. and Sim.) Leon., *P. cryptogea* Pethyb. and Loff., *P. Dreschsleri* Tuck., *P. fagopyri* Takemoto, *P. palmivora* Butler, and *P. parasitica*. Dast.

The fungi were grown in 25 ml. of liquid medium in 150 ml. Erlenmeyer flasks of pyrex glass at room temperature (18–24° C). The media were sterilized at 110° C for 20 minutes unless otherwise noted. The stock cultures were grown on oatmeal agar or potato dextrose agar. A bit of mycelium, a millimeter or two in diameter was used as inoculum, care being taken to avoid including any of the agar of the stock cultures with the inoculum. The commercial asparagine was purified for some experiments by repeated solution in water and precipitation with alcohol. The thiamin was Merck's synthetic betabion; the thiazole was 4-methyl-5-hydroxyethylthiazole and the pyrimidine, 2-methyl-5-bromomethyl-6-aminopyrimidine hydrobromide. Both the latter compounds were generously supplied by Merck and Co. through the courtesy of R. R. Williams.

The amount of thiamin or its intermediates added per flask is expressed in units. One unit is  $10^{-9}$  Mole. All cultures were grown in triplicate.

Two basic media were employed: solution C, consisting of 0.5%  $\text{MgSO}_4 \cdot 7\text{H}_2\text{O}$ , 1.5%  $\text{KH}_2\text{PO}_4$ , 0.05%  $\text{NH}_4\text{NO}_3$ , 1.5% asparagine and 5% dextrose; solution D which contained per liter 1 g  $\text{KNO}_3$ , 1 g  $\text{NH}_4\text{NO}_3$ , 0.5 g  $\text{KH}_2\text{PO}_4$ , 0.25 g  $\text{MgSO}_4 \cdot 7\text{H}_2\text{O}$ , 25 g dextrose and Steinberg's mineral supplements (14) as follows: 0.02 ppm. Mo, 0.05 ppm. Fe, 0.04 ppm. Cu, 0.18 ppm. Zn and 0.02 ppm. Mn.

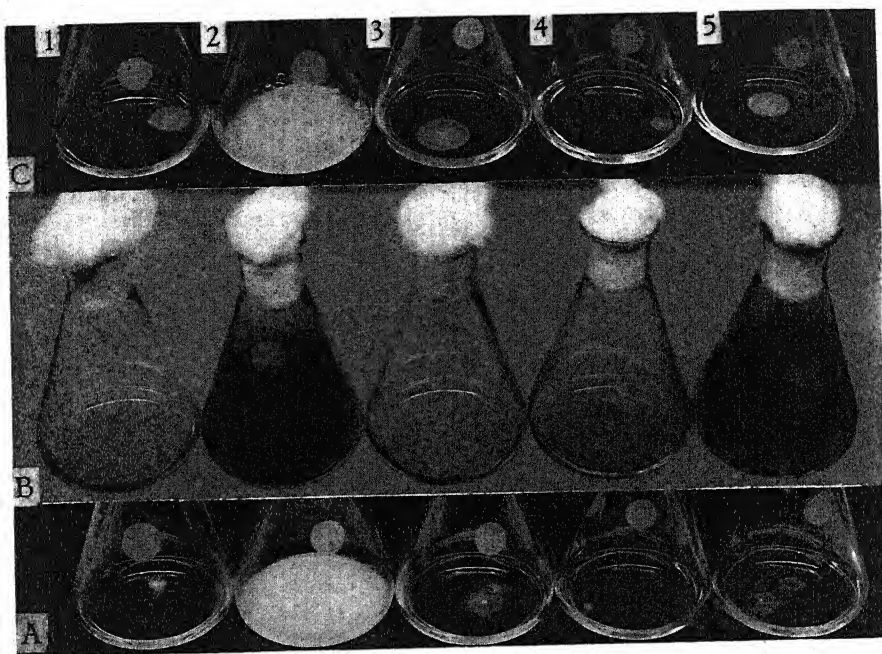


Fig. 1. Fungi grown in, (1) solution C and the same solution plus, (2) 30 units thiamin, (3) 30 units thiazole, (4) 30 units bromo-pyrimidine; (5) 30 units thiazole and 30 units bromo-pyrimidine. A = *Phytophthora cinnamomi*, B = *Phycomyces Blakesleeanus*, C = *Phytophthora Boehmeriae*.

#### EXPERIMENTAL

When these species of *Phytophthora* were grown in (1) solution C, in solution C supplemented with (2) 30 units of thiamin, (3) 30 units of thiazole, (4) 30 units of pyrimidine or (5) a mixture of 30 units of each of the two intermediates the following results were obtained:

*P. cactorum*, *P. citrophthora* and *P. palmivora* showed little growth in solution C or in solution C supplemented with one or both of the intermediates. In the thiamin solutions, however, all three grew slowly but continuously and at the end of a month had formed heavy colonies from 1.5 to 3 cm. in diameter. The dry weight of the mycelium from thiamin cul-

tures of *P. citrophthora* at the end of 51 days was 154 mg., while that in solution C or solution C supplemented with thiamin intermediates averaged 4.0 mg. *P. Boehmeriae*, *P. capsici*, *P. cinnamomi* and *P. parasitica* also failed to grow appreciably in the solutions lacking thiamin; they grew (more rapidly than the species already referred to) in the solutions which contained thiamin.

At the end of a month the colonies of *P. Boehmeriae* in the thiamin solution nearly filled the liquid and their average dry weight was 179.0 mgms. (fig. 1). Those in the solutions lacking thiamin were from 0.5 to 1.0 cm. in diameter and averaged 7.2 mg. The colonies of *P. capsici* also had filled the liquid of the thiamin cultures and averaged 419.6 mg. in dry weight. In the solutions lacking thiamin the colonies ranged from 0.5 to 1.0 cm. in diameter and averaged 0.3 mg. in dry weight.

*P. cinnamomi* grew rapidly in the solutions containing thiamin and the average dry weight after 30 days was 547.2 mg. In the solutions lacking thiamin the colonies ranged from 0.5 to 1.5 cm. in diameter and averaged 1.2 mg. (fig. 1). *P. parasitica* also grew in the thiamin solutions attaining an average dry weight of 114.2 mg. while in the solutions lacking thiamin the average dry weight was 0.4 mg. *P. fagopyri* grew well in the solutions containing thiamin, those containing pyrimidine and those containing the mixture of pyrimidine and thiazole (8). Little or no growth developed in solution C or solution C supplemented with thiazole.

From this experiment it appeared that the growth of at least seven species of *Phytophthora* was markedly improved by the addition of thiamin to the basic solution and but little affected by the addition of the intermediates singly or together. *P. fagopyri* differed from the other species in requiring for satisfactory growth thiamin or its intermediate pyrimidine. It appeared probable that the vitamin was the effective agent because we had used in some of the cultures thiamin which had been filtered sterile; this eliminated the possibility that the vitamin had been split into its intermediates in the sterilization.

It might be suggested, however, that the failure of these organisms to grow satisfactorily in the solutions containing the intermediates was the result of their toxicity at the concentrations used (30 units in 25 ml. solution); not to the inability of the fungi to utilize them.

Two species, *P. capsici* and *P. cinnamomi*, were, therefore, grown in (1), solution C and in the same solution supplemented with (2), 5 units of thiamin; (3), 5 units of thiamin and 30 units of thiazole; (4), 5 units of thiamin and 30 units of pyrimidine; (5), 5 units of thiamin and 30 units of both the thiazole and pyrimidine. The thiamin was filtered sterile and added to the solutions which had been sterilized by heat. Both species

grew rapidly in the solutions containing thiamin and no significant difference was observed between the growth in the presence of the thiamin alone and that in the solutions containing thiamin and its intermediates. This is shown by the dry weight of the mycelium in table 1. The growth in the solutions without thiamin was slight, probably at the expense of material present in the inoculum. In all other solutions it was heavy, the differences between the various solutions containing thiamin falling within the range of probable error.

The more rapid growth in this experiment was because purified asparagine was used in place of the commercial product. Some samples of the latter were found to contain injurious materials and even traces of thiamin or its intermediates. In order to eliminate the effect of the asparagine entirely solution D was used.

TABLE 1

Dry weights of mycelium per flask in solution C and in solution C supplemented with thiamin and its intermediates. Period of growth for *P. cinnamomi* 9 days, and for *P. capsici* 16 days.

SOLUTION  ORGANISM	DRY WT. (MG.) MYCELIUM IN SOLUTION C PLUS				
	Nothing	5 units thiamin	5 units thiamin 30 units thiazole	5 units thiamin 30 units pyrimidine	5 units thiamin 30 units each thiazole and pyrimidine
<i>P. cinnamomi</i>	0.3	334	264	302	297
<i>P. capsici</i>	2.0	152	166	160	178

The various species of *Phytophthora* were grown in (1), solution D and in solution D supplemented with (2), 5 units thiamin; (3), 5 units thiazole; (4), 5 units pyrimidine; (5), 5 units of both thiazole and pyrimidine, and in (6), the sugar solution without mineral salts or supplements. All species, except *P. fagopyri*, grew very little in solution D or in the solutions supplemented with one or both intermediates. The growth in the sugar solution was somewhat less than that in solution D. The growth in the thiamin solutions was several times that in solution D or solution D supplemented with one or both intermediates, though not nearly as great as in solutions containing asparagine. The dry weights are given in table 2.

The growth of *P. fagopyri* was about the same in solution D plus thiamin, plus pyrimidine or plus both intermediates (7 to 12 mg.) and distinctly more than in solution D, solution D plus thiazole or the sugar solution alone (3 to 4 mg.).

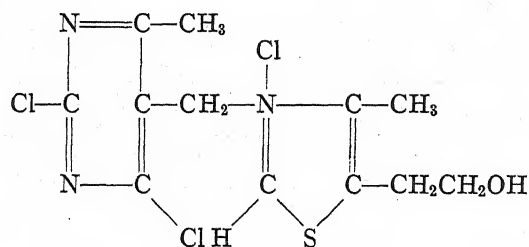
A compound resembling vitamin B<sub>1</sub> was secured through the courtesy of Andrew Bowman of Oxford University. As shown by the structural

TABLE 2

Dry weight of mycelium per flask in solution D plus 5 units of thiamin and in the same solution plus one or both intermediates or no supplements.

ORGANISM	DRY WT. MG. IN SOLUTION D PLUS		PERIOD OF GROWTH DAYS
	Thiamin	Plus intermediates or no supplement	
<i>P. Boehmeriae</i>	11.0	1	35
<i>P. cactorum</i>	6.0	1.5	27
<i>P. cambivora</i>	4.0	0.5	35
<i>P. capsici</i>	18.0	4.0	27
<i>P. cinnamomi</i>	52.0	5.0	27
<i>P. citrophthora</i>		not weighed	
<i>P. cryptogea</i>	41.0	0.3	35
<i>P. Drechsleri</i>	28.0	3.0	27
<i>P. palmivora</i>	11.0	0.3	35
<i>P. parasitica</i>	10.0	0.5	35

formula below the thiazole portion of the compound is identical with the vitamin thiazole but the pyrimidine portion is not.



Bowman's compound is ineffective as a substitute for thiamin. *Phycomyces*, however, is apparently able to split it into its components (10) and to combine the thiazole thus secured with a vitamin pyrimidine to form the essential thiamin (fig. 2). If we are correct in assuming that the species of *Phytophthora* studied here (except *P. fagopyri*) are unable to synthesize thiamin from its intermediates, then Bowman's compound with or without added vitamin pyrimidine should be ineffective. We have tested this hypothesis with one species only.

*P. cinnamomi* grew well in solution C supplemented with 5 units of thiamin, attaining a dry weight of 227 mg. in 11 days. In solution C, in solution C supplemented with 5 units of Bowman's compound or with 5 units of Bowman's compound and 10 units of the bromopyrimidine, little or no growth occurred. In the latter solutions the dry weight of the mycelium averaged between 0.3 and 0.9 mg. (fig. 2). The thiamin and Bowman's



compound were filtered sterile and added to the solutions which had been sterilized with heat.

#### DISCUSSION

Ten of the eleven species of *Phytophthora* studied apparently required an external supply of thiamin and were unable to utilize the intermediates of the vitamin. It appears that these fungi are unable to synthesize the vitamin from its intermediates as *Phycomyces Blakesleeanus* seems to do readily. The synthesis of the vitamin from its intermediates may be enzy-

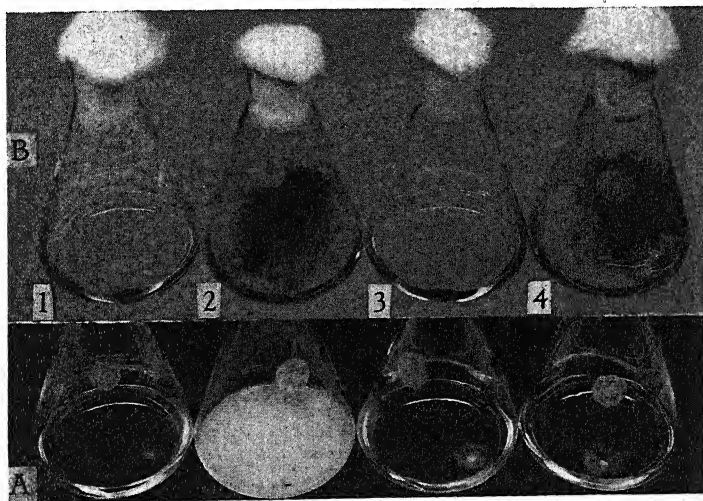


Fig. 2. Fungi grown in, (1) solution C and the same solution plus, (2) 5 units thiamin; (3) 5 units Bowman's compound; (4) 5 units Bowman's compound plus 10 units bromopyrimidine. A = *Phytophthora cinnamomi*, B = *Phycomyces Blakesleeanus*.

matic and these organisms may lack the necessary enzyme. *Phytophthora fagopyri*, on the other hand, seems able not only to synthesize thiamin from its intermediates but to form one of the intermediates from the more elementary materials of the medium (8). In view of the marked difference between the physiology of this species and the others studied, the question may be asked whether *P. fagopyri* is correctly placed in the genus *Phytophthora*.

Our results show that various species of *Phytophthora* are able to grow slowly in a medium which lacks organic nitrogen if the medium is supplemented by thiamin. Kögl and Fries (1) found similar results with *P. cactorum*. Reports that organic nitrogen (peptone for example) are required by these fungi and that inorganic nitrogen is unavailable are probably because the peptone supplies thiamin. Nevertheless, we secured much

greater growth in media containing asparagine than in one containing inorganic nitrogen only.

Our experience leads us to suggest that for work of the type discussed here commercial samples of asparagine should be purified. Repeated solution in water and precipitation with alcohol may be used. Unless precautions are taken with the asparagine erroneous conclusions may be drawn either because of the presence of toxic contaminants or because of the presence of appreciable amounts of thiamin or its intermediates.

Leonian (2, 3, 4, 5) was of the opinion that the accessory factor required by *P. cactorum* was not thiamin because his preparations were still active when treated in such a way as to destroy the vitamin molecule. It was thought that perhaps Leonian's results could be explained by the activity of the thiamin intermediates (8). However, in our experiments the vitamin alone and not the intermediates was effective. It would seem that the treatments used by Leonian did not destroy the vitamin, a substitute for thiamin exists which is more resistant or the intermediates are effective under conditions other than those we have used.

The discovery of organisms which apparently require an external supply of the vitamin itself, suggests the possibility of determining the presence of thiamin and estimating its amount by their use. In fact, it would appear possible to determine the vitamin and one or both intermediates by the use of suitable organisms. In order to use such a method successfully we need to know more of the relation between amount of vitamin supplement and growth of individual fungi, more of the specificity of thiamin and its intermediates and to use suitable means of eliminating the effect of toxic materials which may be present in natural materials. A scheme such as that given below is suggestive only, and even though found eventually to be impracticable from the standpoint of the actual determination, may be useful in showing the known relations of some fungi to thiamin and its intermediates.

I *Phytophthora cinnamomi*

Positive growth effect = thiamin

No growth effect = both intermediates or  
pyrimidine alone or  
thiazole alone or  
no thiamin nor intermediates. See II

II *Phycomyces Blakesleeanus*

Positive growth effect = both intermediates

No growth effect = pyrimidine alone or  
thiazole alone or  
no thiamin nor intermediates. See III

III *Phytophthora fagopyri*

Positive growth effect = pyrimidine alone

No growth effect = thiazole alone or  
no thiamin nor intermediates. See IV

IV *Mucor Ramannianus*

Positive growth effect = thiazole alone

No growth effect = no thiamin nor intermediates.

SUMMARY

1. The following species of *Phytophthora* apparently required for growth an external supply of thiamin and were unable to use the thiamin intermediates: *Phytophthora Boehmeriae*, *P. cactorum*, *P. cambivora*, *P. capsici*, *P. cinnamomi*, *P. citrophthora*, *P. cryptogea*, *P. Dreschsleri*, *P. palmivora*, and *P. parasitica*.

2. A medium of mineral salts, asparagine, sugar and thiamin was much more favorable than one lacking asparagine.

3. *Phytophthora fagopyri* differed from the other species by growing in a medium supplemented with thiamin or its intermediate pyrimidine.

4. A scheme is suggested for determining thiamin or its intermediates by the use of suitable fungi.

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## The winter buds of *Brasenia*

M. A. CHRYSLER<sup>1</sup>

(WITH ELEVEN FIGURES)

The water shield, *Brasenia peltata* Gmel. has long attracted attention on account of the extraordinary thickness of the gelatinous layer which invests the upper part of its stem, the petioles and lower surface of the leaf blades. The structure of the glandular hairs which secrete the "mucilage" has been described by Schrenk (1888) and Keller (1893), and the chemical nature of the secretion has also been investigated to a certain extent by the first author. Surmises concerning the function of the secretion have been made by Mrs. Arber (1920) and others. The development of the hairs has been worked out by Schrenk (l.c.).

But we have been unable to find any reference to the peculiar propagules or winter buds. This is the more surprising because of the wide distribution of the plant. They are really conspicuous objects as seen from a boat when one rows through a colony of the water shield during the autumn. Appearing as irregular shaped translucent reddish bodies 30–50 mm. in length, attached to the plant at a distance of a few decimeters below the surface of the pond, they at once attract attention. Perhaps these buds are not produced under all climatic conditions,<sup>2</sup> but on two occasions, September of 1930 and of 1936, the writer has collected them at the upper end of Lake Maranacook, Kennebec County, Maine. At this location, near the inlet of the lake, the water was from three to four feet deep, and the current was moderate. The occurrence of the plants was somewhat local, being apparently restricted to this part of the lake. A brief account of the morphology of the buds is presented.

The general features are illustrated in the habit photographs. Figure 1 shows a bud still attached to the parent plant, and not quite mature, while figures 2 and 3 show buds after they have become detached. It may be noticed that the lower end of the organ tapers to a blunt point. When the buds are mature the slightest touch dislodges them and they sink to the muddy bottom of the pond, in this respect resembling the winter buds of *Polamogeton crispus* which was described by Clos in 1856. This habit,

<sup>1</sup> The writer gratefully acknowledges the assistance of Mr. J. M. Seidman in preparation of the material.

<sup>2</sup> That these objects are not rare but need merely to be sought at the right time of year is indicated by the discovery of large numbers of them in Cranberry Lake, northern New Jersey, by my colleague, Dr. M. A. Johnson. This collection was made on October 17, 1937, about a month later in the season than the Maine collections, suggesting that the winter buds are formed when the temperature of a pond has fallen.

coupled with the exceedingly slippery nature of the abundant gelatinous covering, makes the collection of the buds an operation subject to many losses. A bud consists of a thickened stem, dwarf leaves with thickened petioles, and the gelatinous layer which envelops the whole organ with the exception of the upper surface of the leaves. Beneath this translucent coating the general color is reddish.

In order to contrast the structure of the winter bud with that of the normal shoot, it may be mentioned that the creeping stem of the latter gives off one or more slender ascending branches with nodes a few centimetres apart, from which spring the long slender petioles bearing floating blades. These are elliptical in shape, about  $75 \times 50$  mm., and centrally peltate. Toward the end of the summer growth in length of a branch slackens, the internodes becoming successively shorter, but the diameter of the tip region of the stem increases from 2 mm. to as much as 5 mm., having more or less the form of an inverted cone. The visible leaves borne on this region are three or four in number, even five, the basal ones having blades 20-25 mm. long (or even 35 mm.), those near the apex 3-10 mm. long, with a few so small that they cannot conveniently be measured. All leaves of a bud develop very short petioles, hence the whole bud occupies a submerged position. The conduplicate vernation to which Miss Keller (1893) has called attention is quite conspicuous in the younger leaves of a bud. The petioles of these leaves are 2-2.5 mm., in diameter compared with

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#### Explanation of figures

Fig. 1. Winter bud not quite mature, still attached to branch. Slightly reduced.

Fig. 2. Winter bud, detached. Slightly reduced.

Fig. 3. Another winter bud. Axillary buds are present. Slightly reduced.

Fig. 4. Long. section through base of a winter bud, showing a frequent appearance of the region of abscission.  $\times 10$ .

Fig. 5. Trans. section of petiole of a winter bud. The double vascular bundle, cortical canals, storage tissue and abundant secretory hairs are shown.  $\times 16$ .

Fig. 6. Trans. section of stem of a winter bud, on same scale as fig. 5. The two pairs of vascular bundles distinguish this organ.

Fig. 7. Trans. section of normal leaf. The well-developed palisade and large space in the spongy tissue are shown. The section passes through one of the stomata with its large substomatal cavity.  $\times 115$ .

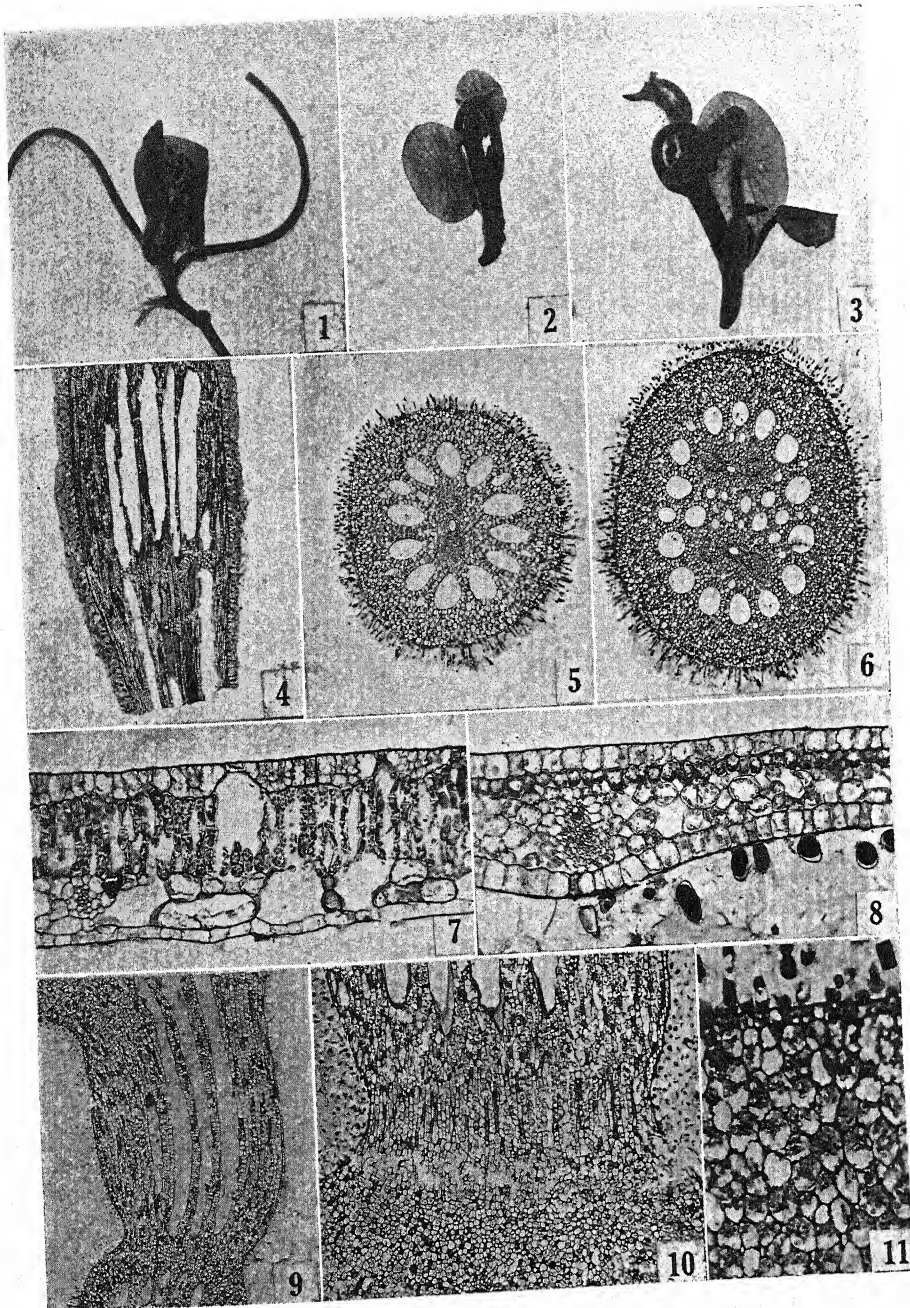
Fig. 8. Trans. section of leaf of a winter bud. The poor development of the palisade and intercellular system, also absence of stomata, are indicated.  $\times 115$ .

Fig. 9. Long. section of a winter bud through the region of abscission.  $\times 10$ .

Fig. 10. Abscission region of another bud, showing breaking away of the cells.  $\times 23$ .

Fig. 11. Portion of epidermis and cortex of stem of a winter bud, showing abundance of starch grains.  $\times 80$ .





1.7–1.8 mm., for the normal leaves. Two or three of the basal leaves may have a well marked secondary bud in the axil. Most of these features are brought out in figures 1–3.

#### STRUCTURE OF THE WINTER BUD

*Blade.* The thickness of the blade of a bud leaf is about 0.17 mm., compared with 0.22 mm. in the floating leaf, that is, about three-fourths as thick. But the structure as brought out by figures 7 and 8 differs in several essential respects. The bud leaf has a more compact mesophyll, lacking extensive intercellular spaces, it entirely lacks the stomata which are characteristic of the upper surface of the floating leaf, and it has only one poorly developed palisade layer in place of the three layers found in the floating leaf. The cells representing the palisade layer are in the bud leaf very short cylinders about  $37 \times 24\mu$ , i.e., about 3:2, while each of the palisade cells of the floating leaf is about the same length but is only  $10\mu$  wide, i.e., nearly 4:1. Thus the tissues do not reach the extreme degree of reduction seen in the submerged leaves of certain species of *Potamogeton*, e.g., *P. pulcher* Tuckerm. The absence of stomata in the bud leaves is no doubt associated with the submerged position, while the compact tissues are adapted to storage rather than photosynthesis, for the abundant plastids are loaded with starch. The reddish color already mentioned is due to the presence of anthocyanin in certain of the cells. The secretory hairs occur only on the lower surface, and are exceedingly numerous, producing a layer of gelatin from two to three times as thick as the leaf.

*Petiole.* This organ is plainly given over to storage, as is shown by the large starch grains which replace chloroplasts. These grains occur in all tissues, although noticeably scarce in the phloem, in which region the grains are small. The proportion of solid tissues to intercellular canals is greater than in the floating leaves, in accordance with specialization for storage. The vascular tissues show the characteristic double phloem and single canal representing xylem. The abundance of secretory hairs may be made out in the photograph (fig. 5.)

*Stem.* Figure 6, from the same bud as the petiole of figure 5, is photographed at the same magnification. The structure is similar to that of the petiole except that in the stem a pair of the double vascular bundles are present. The large amount of starch stored in the cortical cells is shown in the more highly magnified photograph in figure 11. Again the profusion of secretory hairs is evident. These organs are quite scarce in the mature normal stem.

## ABSCISSION

The ease with which the buds may be detached suggests that a mechanism for abscission may be present. Longitudinal sections through the base of a detached bud usually show a clean-cut lower end (fig. 4), looking as though the bud had been cut off by a knife. Sections through buds still attached show a well-marked constriction (fig. 9) at the region of abscission, without necessarily presenting a definite absciss-layer. But in another example, in which the bud was apparently just ready to drop off, zones immediately above and also below nodes were observed in which the cell-walls had changed their composition, as was shown by their taking the safranin stain in place of the fast green typical of the walls of the other internodal cells. Many of these altered cells were breaking down, as is shown in figure 10. Such a zone may be definitely identified as an absciss-layer, comparable to the layer developed by deciduous trees. Longitudinal sections through the base of a bud show the altered condition of cell-walls for some distance back of the break in the case of the phloem cells. These cells moreover are filled with a more or less granular substance which also takes the safranin stain.

## TEMPERATURE RELATIONS

Normally, the buds rest during the winter on the muddy bottom of a pond, where the temperature would not fall below 4°C, on account of the slight current which would at any rate be present at the station in which the collections were made. An attempt was made to carry over some of the buds through the winter in the laboratory, by immersing them in a jar of water placed in an electric refrigerator. This material was kept in the refrigerator from September until March. Unfortunately the jar was shifted by an assistant to a position quite near the freezing element, with the result that the jar was found filled with ice. The temperature of the jar was slowly raised, and some days later the buds were transferred to a shallow glass dish and placed in a window. The buds soon softened and decayed. Obviously all that can be inferred is that the buds are killed by temperatures slightly below freezing point.

The result of this experiment corresponds with those of the extended investigation by Glück (1906), who tried the effect of various temperatures on a variety of winter buds, not including *Brasenia*, however.

## GERMINATION

The object of our attempt to carry the buds over the winter was primarily to observe the growth from the bud after the resting period. The

only observations at present possible are due to the transfer of part of the material from the cold water of the Maine pond to the warmer water of the New Jersey water supply, which took place upon arrival of the material in the laboratory in September 1936. It was noticed that after lapse of a few days some of the buds showed an elongation of the terminal part of the axis, producing a slim shoot as yet devoid of normal leaves. This observation is definitely in contrast to the mode of "germination" shown in *Potamogeton crispus*, as reported and figured by Sauvageau (1893); in this plant the new shoots are produced in one or two of the axils of the winter bud. (A further attempt will be made to clear up the "germination" stages.)

#### NOMENCLATURE

Different terms have been proposed for what we have called "winter buds." "Hibernaculum" is a good but rather clumsy equivalent. The organs evidently belong to the category of "propagules," but this word does not express the whole idea. Mrs. Arber uses the term "turion" when referring to *Potamogeton crispus* (1920, p. 362). Glück (1906) appears to have been the first to use this term in the sense of the winter bud of an aquatic plant—a usage constituting a rather surprising extension of the meaning expressed for example in the definition of turion by Willis (1931): "a scaly sucker or shoot from the ground." At any rate Glück postulates the characters of the turions of water plants (p. 83), and proceeds to distinguish five classes, the distinctions based on whether the modified leaves represent a complete leaf, a petiole, or stipules. It is rather difficult to fit the winter bud of *Brasenia* into any of Glück's classes, because this bud is really a condensed apical part of a shoot rather than a scaly organ having the essential buds located in the axils of protecting scales. *Brasenia* on the contrary appears to depend largely on its thick coat of gelatin for what protection its buds need. In fact it is doubtful whether we should apply the term "turion" to the winter bud of this plant. Even then it corresponds to Glück's definition in two respects, viz., separation from the parent plant, and germination apart from the parent.

#### SUMMARY

In autumn *Brasenia* produces condensed apical organs which are here called "winter buds." With their heavy coating of gelatinous material they are detached from the parent plant by means of an absciss-layer, and fall to the bottom of the pond where they spend the winter. The form and

internal structure of these organs are described. The application of the term "turion" to these winter buds is discussed.

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## Notes on Myxophyceae, I—IV<sup>1</sup>

FRANCIS DROUET

In these Notes, herbaria in which specimens are cited are indicated by the following abbreviations: D, my personal herbarium; F, Farlow Herbarium of Harvard University; G, Herbarium of Goucher College; L, Rijksherbarium, Leiden; Mo. Missouri Botanical Garden; N, New York Botanical Garden; S, Naturhistoriska Riksmuseet, Stockholm; T, Herbarium of Wm. Randolph Taylor. This work was done in part at Yale University with the aid of the Theresa Seessel Research Fellowship.

### I. NOMENCLATURAL CONSIDERATIONS

*Johannesbaptistia pellucida* (Dicki) W. R. Taylor & Drouet, comb. nov. *Hormospora pellucida* Dickie, Journ. Linn. Soc. Bot. **14**: 365 (1874). *Cyanothrix primaria* Gardn., Mem. New York Bot. Gard. **7**: 31, pl. 6, f. 57 (1927). *C. Willei* Gardn., loc. cit., pl. 6, f. 58 (1927). *Nodularia? fusca* W. R. Taylor, Carnegie Inst. Wash. Papers Tortugas Lab. **25**: 48, pl. 1, f. 23 (1928). *Johannesbaptistia primaria* DeToni f., Noterelle nomencl. algolog. **1**: 6 (1934); Drouet descr. emend., Univ. So. Calif. Publ. Hancock Pacific Exped. **3**: 16, pl. 2, f. 3, 4 (1936). *J. Willei* DeToni f., loc. cit. (1934). *J. Gardneri* Frémy, Bull. Soc. Hist. nat. Afr. Nord **26**: 95, pl. x (1935).—Specimens examined: BRAZIL: in rock pools, mixed with *Cladophora* &c., Fernando de Noronha, H. N. Moseley [*Challenger Expedition*] No. 22 (Type of *Hormospora pellucida* in British Museum). VIRGIN ISLANDS: lagoon, Charlotte Amalie, W. A. Hoffman 146593, Sept. 1937 (D, T). PUERTO RICO: San Juan, Lake Tortuguero, N. Wille 830b (TYPE of *Cyanothrix primaria*), 830e (TYPE of *C. Willei*), 844e, 849c, 5 Feb. 1915 (all in Herb. New York Bot. Gard.). FLORIDA: Dry Tortugas, among other filamentous algae, W. R. Taylor, July 1925 (TYPE of *Nodularia? fusca* in Herb. W. R. Taylor) ECUADOR: Galapagos Islands, Isabela Island, W. R. Taylor 123, 12 Jan. 1935 (D); Fernandina Island, Taylor 155, 14 Jan. 1935 (D). CALIFORNIA: in brackish water west of Newport Beach, G. J. Hollenberg 1533e, 26 Sept. 1934 (D, Hollenberg).

During a visit in London in 1937, Prof. Wm. R. Taylor discovered the original material of *Hormospora pellucida*, recognized its similarity to his own *Nodularia? fusca*, and at once communicated his notes to me. More recently, through the great kindness of Messrs. G. Tandy and J. Ramsbottom of the British Museum (Natural History), I was permitted to

<sup>1</sup> Contribution from the Osborn Botanical Laboratory of Yale University and from the Department of Botany, Marine Biological Laboratory.

to examine a portion of this same material. The filaments are excellently preserved and match in every respect those of the types of *Cyanothrix primaria* and *C. Willei*. Prof. G. J. Hollenberg has obligingly sent me material of his collection from California cited above. Frémy (loc. cit.) and Seurat & Frémy, idem 28: 294 (1937), have reported specimens answering to the description of this species from Tunisia, Algeria, and the Dutch West Indies under the superfluous name (cf. Art. 50 of the present International Rules) *J. Gardneri*. In view of its very wide distribution in saline waters of tropical and subtropical regions of the earth, we should not be surprised to discover that this species had been recognized and described at a date far earlier than 1927, when *C. primaria* Gardn. was published.

SCHIZOTHRIX MEXICANA Gom., Ann. Sci. nat. VII Bot 15: 304 (1892). *Lyngbyopsis Willei* Gardn., Mem. New York Bot. Gard., 7: 55, pl. 11, f. 1 (1927).—Specimens seen: PUERTO RICO: on rocks in a brook 5 km. north of Utuado, N. Wille 1597, 8 Mar. 1915 (TYPE of *Lyngbyopsis Willei* in Herb. New York Bot. Gard.). JAMAICA: on rock in 'Wag Water,' Castleton, J. E. Humphrey, 12 Apr. 1893 (F, G).

The type of *L. Willei* represents truly a species of *Schizothrix* and answers in every respect to Gomont's description of *S. mexicana*. The sheaths are thin and very hyaline, but their nature is easily demonstrated when colored blue by treating with chlor-zinc-iodine<sup>2</sup> or when stained lightly with dilute solutions of various dyes. Even after long and meticulous searching in the type material, I am unable to discover the interwoven branching of filaments described as peculiar to the monotypic genus *Lyngbyopsis* Gardn. (ibid. 54). Hormogonial masses are present, and it is possible that the branching of filaments in such masses was studied in an unstained condition. Unfortunately I have not had the opportunity to examine authentic material of *S. mexicana* annotated by Gomont; but there can be little doubt, judging from Gomont's description, that the two types are similar. The Jamaican collection cited above is the one reported by Collins in Proc. Amer. Acad. 37: 240 (1901).

PHORMIDIUM PENICILLATUM<sup>3</sup> Gomont in Jadin, Bull. Soc. Bot. France 40: clix (1893). *Symploca profunda* W. R. Taylor, Carnegie Inst. Wash. Papers Tortugas Lab. 25: 47, pl. 1, f. 18 (1928). *Oscillatoria maricola* Gardn., New York Acad. Sci. Sci. Surv. Porto Rico 8: 270, pl. 1, f. 3 (1932).—Specimens examined: FLORIDA: dredged, White Shoal Sta. 3, Dry Tortugas, W. R. Taylor 254, 11 July 1924 (TYPE of *Symploca profunda* in

<sup>2</sup> For the method of employing this reagent in Myxophycean studies, see Drouet, Amer. Journ. Bot. 24: 604, footnote 7 (1937).

<sup>3</sup> The original spelling is 'penicellatum.'

Herb. W. R. Taylor); dredged, Loggerhead Key, Dry Tortugas, *Taylor 284*, 12 July 1924 (T); dredged beyond Southwest Channel in 20 fathoms, Dry Tortugas, *Taylor 723*, 11 June 1925 (T). PUERTO RICO: Culebra Island, *M. A. Howe 4366*, 7 Mar. 1906 (N); Muertos Island (Caja de Muertos), *Howe 7479*, 8 July 1915 (TYPE of *Oscillatoria maricola* in Herb. New York Bot. Gard.); east of mouth of Guanica Harbor, *Howe 7311*, 1 July 1915 (N); dredged, mouth of Guanica Harbor, *Howe 7446*, 4 July 1915 (N). JAMAICA: 'Blue Hole,' shaded shallow water, *A. E. Wight*, 26 May 1906 (det. Gomont: D, F, S).

The two species proposed here as synonyms of *P. penicillatum* are based upon morphologically similar types, and I am unable to find characters to separate these types from the Jamaican specimens annotated by Gomont as *P. penicillatum*. All the specimens cited above consist of penicillate plant masses from salt water, principally below low tide level; the cells have rose- or violet-colored protoplasm and are usually longer than broad; the calyptra of the apical cell is rather inconspicuous and rotund or depressed-conical. Gomont's type from Réunion was described as having trichomes  $6\mu$  in diameter; the Antillean material seen here has trichomes ranging from  $5.5\mu$  to  $9\mu$  in diameter.

## II. MYXOPHYCEAE FROM COSTA RICA

A small package of blue-green algae from Costa Rica was recently sent to me for study by Dr. Carroll W. Dodge of the Missouri Botanical Garden. I interpret the specimens as follows, listing them under specific names according to provinces:

*CALOTHRIX CONTARENII* (Zanard.) Born. & Flah., *Ann. Sci. nat. VII Bot. 3*: 355 (1886).—One collection on wood in salt water, PUNTARENAS: along seashore between Río Sándoval and Río Tigre, *Dodge 4357*, 1 May 1930 (D, Mo).

*CALOTHRIX PILOSA* Harv. ex Born. & Flah., *ibid.* 363 (1886). *Tildenia pilosa* Polj., *Bull. Jard. Bot. Princip. U.S.S.R.* 27: 227 (1928). *Setchelliella pilosa* DeToni f., *Noterelle nomencl. algolog. VIII* (1936).—On wood in salt water, PUNTARENAS: along seashore between Río Sándoval and Río Tigre, *Dodge 4537A*, 1 May 1930 (D, Mo).

*FREMYELLA VITIENSIS* (Born. & Flah.) DeToni f., *loc. cit.* (1936). *Microchaete vitiensis* Ask. ex Born. & Flah., *ibid.* 5: 84 (1887).—Marine, PUNTARENAS: along seashore between Río Sándoval and Río Tigre, *Dodge*, 1 May 1930 (D, Mo).

*SCYTONEMA HOFMANNII* Ag. ex Born. & Flah., *ibid.* 97 (1887).—On tree trunks, often somewhat lichenized. ALAJUELA: la Palma de San Ramón, *A. M. Brenes 176, 177*, 12 Nov. 1920 (D, Mo). LIMON: on

Croton at house, Hamburg Farm, *Dodge & F. Nevermann* 7454, 31 Mar. 1930 (Mo).

*SCHIZOTHRIX THELEPHOROIDES* (Mont.) Gom., *idem* 15: 319, pl. x, f. 1-4 (1892).—On soil and mixed with other algae, mosses, and lichens, ALAJUELA: Alto del Mendongo del San Ramón, *A. M. Brenes* 285, 9 Jan. 1930 (D, Mo).

*OSCILLATORIA ANIMALIS* Ag. ex Gom., *ibid.* 16: 227, pl. vii, f. 11 (1892).—On wet mosses with juvenile *Nostoc* sp., SAN JOSE: potreros of Rancho Redondo, *Dodge & W. S. Thomas* 5267, 18 Nov. 1929 (D, Mo).

### III. MYXOPHYCEAE FROM ARGENTINA

During the period November 1936 until January 1937, Dr. Stillman Wright was engaged in a limnological survey of some freshwater lakes of central Argentina, under the joint auspices of the División de Piscicultura of Argentina and the Comissão Technica de Piscicultura of Brazil. His formalin-preserved material, sent to me for study and distribution, consists of the following specimens, cited geographically under the specific names according to provinces. Serial numbers of collections in *italics* are to be understood as those of Dr. Wright.

*MICROCYSTIS AERUGINOSA* Kütz., Tab. phyc. 1: 6, Tab. 8 (1845-49).—Abundant in the plankton of many lakes, BUENOS AIRES: Laguna Los Chilenos near Dufaur, 2113, 11 Jan. (D); Laguna Blanca Grande, 2098, 14 Jan. (D, F, L, N, S); Laguna Chascomus, 2101, 11 Nov. (D). SAN LUIS: with *Phormidium mucicola*, Laguna Tala, 2111, 10 Dec. (D, F, L, S); with *P. mucicola*, Laguna Garcia, 2096, 7 Dec. (D, L, N, S); with *P. mucicola*, Laguna La China, 2112, 4 Dec. (D, L, N, S); with *P. mucicola*, Primera Laguna, 2059, 4 Dec. (D).

*CALOTHRIX PARIETINA* (Näg.) Thur. ex Born. & Flah., *Ann. Sci. nat. VII Bot.* 3: 366 (1886).—In an incrustation on a fish tank, BUENOS AIRES: Chascomus, 2102, 19 Nov. (D, F, L, N, S).

*GLOEOTRICHIA NATANS* (Hedw.) Rabenh. ex Born. & Flah., *ibid.* 4: 369 (1886).—One collection, SAN LUIS: Laguna Viejo, 2094, 8 Dec. (D, F, L, N, S).

*ANABAENA ?FLOS-AQUAE* (Lyngb.) Bréb. ex Born. & Flah., *ibid.* 7: 228 (1888).—The material is without spores, and I therefore assign the specific name with some uncertainty. Forming a considerable part of the plankton from one lake, SAN LUIS: Tres Lagunas (No. 3), 2110, 6 Dec. (D, F, L, N, S).

*APHANIZOMENON FLOS-AQUAE* (L.) Ralfs ex Born. & Flah., *ibid.* 241 (1888).—From the plankton, BUENOS AIRES: Laguna Carlito, Necochea, 2093, 17 Jan. (D, F, L, N, S).

PLECTONEMA NOSTOCORUM Born. ex Gom., idem 16: 102, pl. i, f. 11 (1892).—With *Calothrix parietina* in an incrustation on a fish tank, BUENOS AIRES: Chascomus, 2102, 19 Nov. (D, F, L, N, S).

PHORMIDIUM MUCICOLA Naum. & Huber in Huber-Pestalozzi & Naumann, Ber. d. d. bot. Ges. 47: 68, f. 1-6 (1929).—I discuss the occurrence of this species in North America in a current number of Rhodora (1938). In the Argentine lakes it is abundant within the sheaths of *Microcystis aeruginosa*, but wholly absent in collections from some of the lakes. BUENOS AIRES: Laguna Los Chilenos near Dufaur, 2113, 11 Jan. (D). SAN LUIS: Laguna La China, 2112, 4 Dec. (D, L, N, S); Laguna Tala, 2111, 10 Dec. (D, F, L, S); Laguna Garcia, 2096, 7 Dec. (D, L, N, S).

OSCILLATORIA PRINCEPS Vauch. ex Gom., ibid. 206, pl. vi, f. 9 (1892). *Lyngbya gigantea* Lewis, Zirkle & Patrick, Journ. Elisha Mitchell Sci. Soc. 1933: 221 (1933).—Two collections, CÓRDOBA: creek near city of Córdoba, 2116, 21 Dec. (D, F, L, N, S); Laguna Embolse Rio III, Almafuerte, 2115, 18 Dec. (D, L, N, S).

OSCILLATORIA ANGUINA Bory ex Gom., ibid. 214, pl. vi, f. 16 (1892). *Phormidium Chungii* Gardn.,<sup>4</sup> Univ. Calif. Publ. Bot. 14: 4, pl. 1, f. 5 (1927).—One collection: CÓRDOBA: Laguna Embolse Rio III, Almafuerte, 2091, 16 Dec. (D, F, L, N, S).

OSCILLATORIA OKENI Ag. ex Gom., ibid. 232, pl. vii, f. 18 (1892).—Specimens seen: BUENOS AIRES: Australian tank, Estancia "La Lola," Dufaur, 2092, 13 Jan. (D, F, L, N, S). SAN LUIS: Laguna El Sarco, 2106, 7 Dec. (D). CÓRDOBA: with *O. anguina*, Laguna Embolse Rio III, Almafuerte, 2091, 16 Dec. (D, F, L, N, S).

OSCILLATORIA CHALYBEA Mert. ex Gom., ibid. 232, pl. vii, f. 19 (1892); Borge, Ark. f. Bot. 6(4): 11 (1906).—Specimens seen from Argentina: JUJUY: with *Phormidium laminosum*, Quinta, in aqua 36.5° [C], R. E. Fries (Regnell Expedition) No. 9, 12 June 1901 (S). CÓRDOBA: with *O. anguina*, Laguna Embolse Rio III, Almafuerte, 2091, 16 Dec. (D, F, L, N, S).

OSCILLATORIA SPLENDIDA Grev. ex Gom., ibid. 224, pl. vii, f. 7-8 (1892).—BUENOS AIRES: with *O. Okeni*, Australian tank, Estancia "La Lola," Dufaur, 2092, 13 Jan. (D, F, L, N, S).

SPIRULINA PLATENSIS (Gom.) Geitl., Rabenh. Kryptogamen-Fl. 14:

<sup>4</sup> The trichomes of the TYPE of *P. Chungii* in the Farlow Herbarium (CHINA: Fulung Hot Springs, Tanggate, Foochow, *Chung* 4452) are indistinguishable from those of other specimens placed under the name *O. anguina* in my herbarium. The trichomes are mixed with filaments of other sheathed Myxophyceae, but I am unable to demonstrate sheath material (except in hormogonial masses) belonging properly to *P. Chungii*.



925, f. 589, 590 (1932). *Arthrospira platensis* (Nordst.) Gom., *ibid.* 247, pl. vii, f. 27 (1892). *S. Jenneri* var. *platensis* Nordst. ex Gom., *loc. cit.* (1892); Nordst. in Wittr. & Nordst., *Alg. exs.* 14: 679 (1884), in Farlow *Herb.*—The original material of this species was collected in Uruguay by Arechavaleta and distributed in the exsiccata noted above. Several workers have since reported collections from Africa. Miss Rich in *Rév. algol.* 6(1): 75–79 (1931) has given us detailed observations upon her material from Kenya Colony. She reports that in a considerable number of individuals the trichomatal dimensions vary within a much wider range than that noted in Gomont's description. Gomont, of course, based his diagnosis upon a single dried collection from another continent. As did the African collections, the material cited here comes from highly alkaline lakes: SAN LUIS: with *Anabaena ?flos-aquae*, Tres Lagunas (No. 3), 2110, 6 Dec. (D, F, L, N, S); Laguna El Chorriado, 2089, 10 Dec. (D, F, L, N, S).

SPIRULINA MAJOR Kütz. ex Gom., *ibid.* 251, pl. vii, f. 29 (1892). *S. densa* Lillick, *Amer. Midl. Nat.* 16: 210, f. 1A (1935).—Two collections: BUENOS AIRES: with *Oscillatoria Okeni*, Australian tank, Estancia "La Lola," Dufaur, 2092, 13 Jan. (D, F, L, N, S). SAN LUIS: Laguna El Sarco, 2106, 7 Dec. (D).

#### IV. NORTH AMERICAN MYXOPHYCEAE IN THE SCHWEINITZ HERBARIUM

During a recent visit at the Academy of Natural Sciences in Philadelphia, Dr. F. W. Pennell and Dr. Ruth Patrick invited me to look through the rather large algal collections of Dr. Lewis David von Schweinitz (1780–1834). The Myxophyceae, although few in number, are chiefly freshwater forms collected in the vicinity of Winston-Salem, North Carolina, presumably between the years 1812 and 1821; some specimens come from other states. Few data appear upon the specimens themselves; beyond a generic or specific name, there is usually only a terse note "Salem" for what is now Winston-Salem, "Virg" for Virginia, "Beth" for Bethlehem, Pennsylvania, etc. Drs. Pennell, Schallert, Benedict, and Barnhart have given us an enlightening symposium on the life and collections of Dr. Schweinitz in *Bartonia* 16: 1–36 (1934). In his unpublished manuscript,<sup>5</sup> "Flora Salemitana" (dated 1821), now on file in the Herbarium of the Academy, Schweinitz has mentioned most of the North Carolina specimens by name and has given a few notes on the locality and habitat of each. In preparing the labels and in citing in the enumeration below, I have included all such information from the above sources as could with some degree of certainty be attached to the specimens individually. In the collection also are specimens of no inconsiderable his-

<sup>5</sup> See Pennell in *Bartonia* 13: 50–52 (1931).



torical interest communicated to Schweinitz by his friend and correspondent, Dr. John Torrey. These are indicated most often by the simple annotation "Torrey," sometimes with a transmittal number, sometimes with more exact data.<sup>6</sup> In the list below, all specimens cited are to be found in the Herbarium of the Academy at Philadelphia and, unless otherwise indicated, are to be understood as collected by Schweinitz himself.

NOSTOC COMMUNE Vauch. ex Born. & Flah., Ann. Sci. nat. VII Bot. 7: 203 (1888).—NORTH CAROLINA: as *N. commune*, common at certain seasons upon the earth, Winston-Salem.

NOSTOC PRUNIFORME (L.) Ag. ex Born. & Flah., ibid. 215 (1888).—PENNSYLVANIA: as "*N. crepitans* Nobis," Bethlehem.

NOSTOC VERRUCOSUM (L.) Vauch. ex Born. & Flah., ibid. 216 (1888).—VIRGINIA: as *N. Botrydium*.

SCYTONEMA GUYANENSE (Mont.) Born. & Flah., ibid. 5: 94 (1887).—UNITED STATES: as *S. atrovirens*, on rocks, comm. Torrey. NORTH CAROLINA: as *Conferva ebena*, Winston-Salem.

PORPHYROSIPHON NOTARISII (Menegh.) Kütz. ex Gom., idem 15: 331, pl. xii, f. 1, 2 (1892).—For a discussion of the morphology and recent synonymy of this species, see Drouet in Amer. Journ. Bot. 24: 601 (1937). NORTH CAROLINA: as *Conferva ericetorum*, on the earth, red, Winston-Salem.

LYNGBYA CONFEROIDES Ag. ex Gom., ibid. 16: 136, pl. iii, f. 5, 6 (1892).—UNITED STATES: as *Bangia atropurpurea*, sea shore, comm. Torrey 189.

LYNGBYA OCHRACEA (Kütz.) Thur. ex Gom., ibid. 149 (1892).—NORTH CAROLINA: in most metallic springs—this from near Pilot [Mountain], near Winston-Salem.

PHORMIDIUM TRELEASEI Gom., Bull. Soc. Bot. France 46: 37 (1899).—The one collection<sup>7</sup> comes from the type locality of the species, ARKANSAS: as *Oscillatoria calida*, hot springs of the Washita [now Hot Springs, near the Ouachita River], 150° F, comm. Torrey.

PHORMIDIUM INUNDATUM Kütz. ex Gom., Ann. Sci. nat. VII Bot. 16: 172, pl. iv, f. 31, 32 (1892). *P. purpurascens* var. *elegans* Drouet,<sup>8</sup> Bot. Gaz.

<sup>6</sup> The correspondence of Schweinitz and Torrey has been published in fairly complete form in Mem. Torr. Bot. Club 16(3) (1921). Unfortunately, lists of collections exchanged between the two men have been omitted; and I have not had the opportunity to hunt for further data on the Torrey specimens among the letters themselves.

<sup>7</sup> It is not clear whether Thomas Nuttall, Thomas Drummond, or Zina Pitcher collected this material. See Mem. Torr. Bot. Club 16: 137, 151, 248, 277, 279 (1921).

<sup>8</sup> The TYPE of *P. purpurascens* var. *elegans* in my personal herbarium (MISSOURI: in a spring at east side of Highway 28 at Gasconade River Bridge, Pulaski

95: 696, f. 3 (1934).—NORTH CAROLINA: as *Oscillatoria fontinalis*, rare in springs on stones, Winston-Salem.

PHORMIDIUM RETZII (Ag.) Gom., *ibid.* 176, pl. v, f. 6-9 (1892).—NORTH CAROLINA: as *Conferva*, Winston-Salem.

PHORMIDIUM SETCHELLIANUM Gom., *ibid.* 190, pl. v, f. 25, 26 (1892).—It is unfortunate that we have no further data on this collection, for the species is known to me only in specimens from New England. UNITED STATES: as *Oscillatoria Friesii*, *comm. Torrey* 353.

PHORMIDIUM FAVOSUM (Bory) Gom., *ibid.* 180, pl. v, f. 14, 15 (1892).—UNITED STATES: as *Oscillatoria fusco-purpurea*, *comm. Torrey* 161. NORTH CAROLINA: as *O. fontinalis*, rare in springs on stones, Winston-Salem.

PHORMIDIUM UNCINATUM (Ag.) Gom., *ibid.* 184, pl. v, f. 21, 22 (1892).—NORTH CAROLINA: as *Oscillatoria flexuosa?*, Winston-Salem.

PHORMIDIUM AUTUMNALE (Ag.) Gom., *ibid.* 187, pl. v, f. 23, 24 (1892). *Lyngbya hahatonkensis* Drouet, *Bot. Gaz.* 95: 698, f. 5 (1934).—NORTH CAROLINA: as *Oscillatoria vaginata*, on the staircase of Barhouse, Winston-Salem.

OSCILLATORIA LIMOSA Ag. ex Gom., *ibid.* 210, pl. vi, f. 13 (1892).—NORTH CAROLINA: as *O. flexuosa?*, Winston-Salem; as *Conferva canalicularis*, a handsome one in Stotz bottom garden, Winston-Salem.

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DEPARTMENT OF BOTANY, MARINE BIOLOGICAL LABORATORY

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County, *Drouet* 1033, 1 Oct. 1932) differs in no respect from the specimen of *P. inundatum* examined by M. Gomont in the Farlow Herbarium, MAINE: on water trough, Eastport, *W. G. Farlow*, Sept. 1877. The violet-black color of the plant mass as described in the original publication of the var. *elegans* is evident only when the mass is observed beneath the surface of the water: out of the water, the color is quite blue-green.

## Notes on Maryland algae<sup>1</sup>

HAROLD C. BOLD  
(WITH PLATES 6 AND 7)

From 1934 through 1937 the author was resident for six weeks each summer at the Chesapeake Biological Laboratory which is located on Solomons Island, Calvert County, Maryland. The following paper contains notes on a study of the algae of that region and descriptions of new species, of forms new to the United States or significant for some other reason. The organisms discussed below are all fresh-water forms and are treated according to the classification given by Smith (1933); all belong to the order Volvocales.

### POLYBLEPHARIDACEAE

*PYRAMIMONAS MONTANA* Geitler (figs. 1-12).—Although eight species of this genus have been described from abroad (Pascher, 1927), but two have been recorded as present in the algal flora of this country. Smith (1933) reports finding *P. tetrarhyncus* Schmarda from Wisconsin lakes and earlier Prescott (1926) reported *P. inconstans* Hodgetts from Iowa. During the past four summers small puddles in the clay mud of a barnyard at Solomons became colored a brilliant green due to the presence of such organisms as *Pandorina morum* Bory, *Eudorina elegans* Ehr., *Chlamydo-botrys stellata* Korsch.; during periods of intense sunlight a bright green cloud of organisms gathered near the surface of the most intensely illuminated portion of each pool and microscopic examination revealed that these streaks consisted practically entirely of *Pyramimonas* sp. Attempts to cultivate the organism have been unsuccessful; preparation of stained slides has been only partially successful and efforts to preserve the organism have failed because of the absence of a cell wall. The pools containing the organism are supplied with water from an artesian well which runs into a trough and overflows on the surrounding clay. At times pools become completely dry but following rains they again become populated with *Pyramimonas* and the associated organisms.

Figures 1-12 illustrate the organism, which seems to be identical with *P. montana* Geitler (Geitler, 1925). The cells are bluntly conical and swim with the base of the cone directed forward. Most of the individuals are slightly four lobed or ridged at the anterior end (figs. 1, 2) but there are all gradations from this condition to cells with almost truncate anterior poles (fig. 12). In ridged individuals there is a depression in the center of the anterior end among the ridges in which the flagella are inserted. The

<sup>1</sup> Contribution Number Sixteen from the Chesapeake Biological laboratory.

cells are rounded in end view and optical transverse section and taper symmetrically toward the posterior. Cell size in my specimens varies from 12 to 20 microns in length and from 8 to 16 microns in width at the broadest point; Geitler's specimens varied from 17 to 22.5 microns. The cells move very rapidly forward turning on their long axes and when they strike another object they rapidly reverse the direction of their movement without reversing the orientation of their bodies. Four flagella are attached to the central region of the anterior end of the cell and are about as long as the length of the cell body. Treatment with weak iodine solution or osmic acid vapor reveals the presence of a small but distinct blepharoplast to which the flagella are attached in such a way that they appear to diverge at approximately  $90^\circ$  angles when the cell is at rest (figs. 3, 8-10). A cell wall is lacking and the cells are therefore somewhat metabolic as indicated by changes in shape when two individuals collide.

On either side of the blepharoplast a contractile vacuole is visible in the living cells (figs. 1, 2, 3 etc.); these contract and expand alternately. The chloroplastid is cup shaped and massive and appears to fill the cell in surface view. In longitudinal optical section it becomes apparent that there is a shallow region of colorless cytoplasm at the posterior pole of the cell in which the nucleus is visible (figs. 2, 5, 7). The chloroplastid in living cells is highly granular and contains scattered starch grains and oil droplets. When the cell is ridged the chlorophyll-bearing cytoplasm extends out into the ridges anteriorly. Deep within the chloroplastid in the basal region of the cell a single pyrenoid is usually embedded; it is rarely entire (figs. 1, 2), usually consisting of a number of fragments or portions (figs. 5, 8, 11). The pyrenoid is usually surrounded by a ring of small starch grains (figs. 1, 2); figure 5a represents a compound pyrenoid as it appears in a cell stained with iodine; each portion consists of a proteinaceous portion, at the periphery of which occurs a violet-stained starch grain. Other starch grains which presumably originate around the pyrenoid, occur in other regions of the chloroplastid.

The nucleus lies in the region of colorless cytoplasm within the chloroplastid and is distinctly pear-shaped (figs. 8, 11); the beak of the nucleus extends between the two contractile vacuoles and lies beneath the blepharoplast. In my specimens the nucleus was not visible in the living cells but became sharply defined when the cells were moribund or when treated with osmic acid, iodine or with haematoxylin after fixation. Each nucleus contains a single large spherical nucleolus and in stained preparations there is some evidence of the presence of a chromatin network.

Hanging drop mounts did not remain in good condition for more than forty-eight hours, probably due to lack of oxygen and to the multiplication

of numerous bacteria. In such cultures some individuals disintegrated, while others rounded up, became enveloped in a thick gelatinous wall, and apparently entered into a period of dormancy (fig. 4).

Multiplication consists of the longitudinal division of one cell into two; dividing individuals were encountered most frequently in collections made late in the afternoon. No details of nuclear division were obtained in fixed preparations; Geitler (1925) figures one stage which indicates that it is mitotic. Aside from actual cleavage there are two criteria which indicate impending cell division. The pyrenoid, whether simple or fragmented, becomes elongated in a plane at right angles to the long axis of the cells (fig. 6). As the time for cytokinesis approaches the elongated mass is gradually separated into two portions (figs. 7, 8) which form the pyrenoids of the daughter cells (figs. 10, 11). A second indication of approaching division is the gradual increase in the number of flagella. The cell figured as 5 had six flagella two of which were shorter and were apparently growing out from the blepharoplast in anticipation of cleavage. Many individuals with eight flagella were seen (figs. 7, 8) in collections examined late in the afternoon and evening, but by the following morning all cells in the culture were again quadriflagellate indicating that cell division had been completed. The cells apparently begin to increase the number of flagella long before cytokinesis is completed or even initiated. In division, as observed in living cells, the flagella begin to diverge into two groups of four as the anterior pole of the cell broadens (figs. 7, 8) and since the contractile vacuoles also diverge growth probably occurs most actively in the region just between them. Each daughter cell therefore receives one contractile vacuole from the mother cell. The posterior portion of the cell subsequently increases in size and a cleavage furrow appears in it (fig. 8). Similarly a furrow is initiated between the groups of diverging flagella and when the furrows meet, cell division is complete. Cells which are still incompletely segregated already contain two contractile vacuoles each (fig. 9), so that one must arise *de novo* very quickly in each. Figure 10 illustrates one product of a recent cell division fixed with osmic vapor. As in other species of the genus, cell division occurs while the organism is motile. The organism described above appears to be very close to Geitler's (1925) *Pyramimonas montana* which he found in an Alpine pool at an altitude of five thousand feet. In *P. montana* Geitler reports that the ratio of length to breadth is that of 2:1 or slightly less than 1; in the Maryland organism it is approximately 8:5, but occasional relatively longer individuals occur. Geitler states that his species was pale yellowish in color while the organisms I observed were a deep grass-green. It is well known however that differences in mineral content of the medium profoundly



affect the intensity of the pigmentation. The Maryland organisms therefore should probably be considered as a form of *P. montana* Geitler; it is here reported for the first time from the United States.

#### CHLAMYDOMONADACEAE

*CARTERIA CRUCIFERA* Korsch. (figs. 16-17).—This organism occurred in considerable abundance during the summer of 1935 in a small lily pool in the garden of a residence at Solomons Island. It has not been seen in succeeding summers but as the drawings indicate it is undoubtedly identical with *C. crucifera* Korsch.<sup>2</sup> The cells among my specimens vary from a minimum of  $10\mu$  to a maximum of  $20\mu$  in length; Korschikoff reports individuals up to  $27\mu$  in length. The outstanding character of the species is the cruciform arrangement of the flagella which originate from the prominently four-parted papilla. The pyrenoid lies on the median longitudinal axis of the cell, deep within the chloroplastid. The latter is cup-shaped, sometimes open also posteriorly and is characteristically striated or ribbed longitudinally. The cells divide while quiescent into groups of four or eight (fig. 17) and these daughter cells when liberated soon achieve the size of the parent cells. The chloroplastid in my specimens was filled with abundant starch grains. The nucleus is located in the posterior third of the cell and lies within the opening of the chloroplastid. The shape of the chloroplastid and the central position of the pyrenoid indicate that the species belongs in the section *Pseudoagloë* Pascher. As far as I can ascertain this organism is reported here for the first time from the United States.

*Carteria ellipsoidalis* sp. nov.—Cellulis vere et semper ellipsoidalibus; chromatophora aperte urceolata; stigmatibus in media parte vel subanteriore chromatophorae; pyrenoide singula grande axiale; nucleo incluso in cytoplasmate sine colore; cellulis sine papilla; vacuolibus contractilibus praesentibus; longitudine cellulae vegetativae  $6-24\mu$ ; ceteris characteribus similibus generi. Propagatio fit 2, 4 aut 8 cellulis intra cellulae matricialis membrum ortis. Hab. In fossa juxta agrum campestrum, Solomons, Calvert Co., Maryland (figs. 18-20).

These organisms were repeatedly collected from barnyard puddles similar to those in which *Pyramimonas montana* occurred. The cells vary from 10 to 25 microns in length and are always truly ellipsoidal in shape. The chloroplastid is very clearly urn- or cup-shaped with the opening usually extending well back toward the posterior half of the cell. There is

<sup>2</sup> Apparently the original publication of this species is in Pascher (1927, p. 157), since it is not found in any of Korschikoff's papers that are available: the case is an example of Pascher's inconvenient habit of failing to indicate species which are described as new.



a single axial pyrenoid which lies near the base of the chloroplastid, the latter being filled with minute starch grains some of which surround the pyrenoid. The stigma is small and located within the anterior third of the chloroplastid. The four flagella are about equal in length to the cell body and are attached to a minute blepharoplast which lies very near the margin of the protoplast. The cell wall is thin and lacks a papilla, and the protoplast is slightly truncated in this region. Cell division is longitudinal and occurs while the cells are in a quiescent condition; four- and eight-celled stages are commonly found (fig. 20). This organism is closely related to *C. globosa* Korsch. from which it differs plainly, however, in its pronounced and constant ellipsoidal form and in the smaller size of its cells. The present species like *C. globosa* belongs to the section EUCARTERIA.

*CHLAMYDOMONAS METASTIGMA* (Stein) Gorosch. (fig. 21).—This organism occurred sparingly in barnyard puddles along with the above species of *Carteria*. It belongs to the sub-genus *Amphichloris* Pascher, and is characterized by the presence of both anterior and posterior pyrenoids which are embedded axially in the urn-shaped chloroplastid. The latter is partially perforated near the equator of the ellipsoidal cell and the stigma is posterior to this opening. The nucleus lies in the central portion of the cell and is often visible through the opening in the chloroplastid. The latter is like a window and does not completely divide the chloroplastid. In my specimens vegetative cells vary in length from 11.8 to 16 microns the cells being slightly smaller than those observed by Goroschankin (1891). The cells lack a papilla; no stages in reproduction were observed.

*Chlamydomonas schizochlora* sp. nov. (figs. 13-15).—Cellulis vegetativis grandibus, 30-40 $\mu$  longitudine, cylindroidibus; anteriore papilla obtusa; chromatophora fissa in multas partes sed in toto urceolata; una pyrenoide in quoque segmento; stigmat lanceolato usque ad 5 $\mu$  flagellis brevibus, minoribus quam dimidio longitudinis cellulae; nucleo sub-anteriore, sphaerico; vacuolibus contractilibus praesentibus. Propagatio non observata est. Hab.: In stagno, Solomons, Calvert Co., Md.

This organism was observed infrequently sparingly mixed with other algae in a small pond or swamp at Point Patience, Calvert County, Md., and is clearly a member of the sub-genus *Pleiochloris* Pascher in which the cells contain many laterally distributed pyrenoids. The cells are elongated, cylindrical-ellipsoidal and relatively large varying from 31-40 microns in length and are somewhat less than half as wide. The posterior and anterior poles are equally rounded. The chloroplastid as a whole is cup- or urn-shape, but is incompletely divided into mosaic-like segments each of which contains a single pyrenoid superficially embedded. The number of chloroplastid segments fluctuate in my specimens between eleven and seventeen.

The stigma is anterior, in edge view pointed at both ends, in face view narrowly elliptical, and may reach a length of 5 microns. Two contractile vacuoles are present beneath the lenticular papilla and below them in the colorless cytoplasm a rather large nucleus is present (figs. 13-15). The two flagella are short, less than one half the length of the cell body and they emerge close together through the broad papilla. The cells I observed were extremely sluggish in their movements, perhaps because of the large size of the cells in relation to the size of the flagella. This organism is closely related to *C. breviciliata* Korsch. from which it is readily distinguishable however by the mosaic chloroplastid and by the anterior position of the extremely elongated stigma and by the more anterior position of the nucleus.

#### PHACOTACEAE

*DYSMORPHOCOCCUS VARIABILIS* Takeda (figs. 22-25).—This organism appeared in great numbers in barnyard puddles along with other Volvocales during the summer of 1936. The genus was described by Takeda (1916) from material collected in a small pool in Surrey, England; Korschikoff (1925) reports the occurrence of *D. variabilis* Takeda and a new species *D. coccifera* in the vicinity of Charkow. As is typical of members of this family, the cells of *Dysmorphococcus* are encased within a lorica which is almost colorless in young individuals but becomes dark brown in more mature cells. The surface of the lorica appears rough under low magnifications but higher magnification reveals the presence of a pattern or sculpturing on the lorica. Takeda reported that this consisted of closely placed granules: "It can be positively stated," he says, "that they are granules, and not scrobiculations." Korschikoff on the contrary reports that the shell in the same species is ornamented not with granules but with true pores which in transverse section, as seen at the surface, appear to be hexagonal. I can substantiate the observations of Korschikoff on this point though there seems to be a high frequency of occurrence of pentagons and other types of polygons in cross sectional views of the pores. An accurate picture of the pores is only obtained through the use of an apochromatic optical system. Under lower magnifications the shell does not appear granulated and I have represented it in this manner in figure 25, below which I have depicted a more detailed segment of a shell. Takeda mentions the occurrence of a "dotted line" running longitudinally around the shell; critical observation convinces me that this is always present and that it consists in reality of a narrow band of wall material in which no pores occur (fig. 23) and along which the splitting of the shell occurs at the time of reproduction. Korschikoff (1925) comes to a similar conclusion in

his studies of *D. coccifera*. The size of the shells which I have observed falls within the specific limits given by Takeda, namely 14-19 microns long and between 13 and 17 microns broad across the flattened surface. The lorica displays a pronounced dorsiventrality, being somewhat flattened in a plane at right angles to the long axis especially posteriorly (fig. 23); it is more rounded usually anteriorly (fig. 24). The flagella of the contained protoplast emerge through two minute openings which are oriented at about 45° angles with reference to a plane parallel to the broad surface of the shell. The protoplast is always smaller than the lorica and is pear-shaped with the colorless beak being attached near the apex of the shell. Along with Takeda and Korschikoff I have been unable to convince myself that the protoplast is walled. Its structure is typically Volvocine: contractile vacuoles, stigma, a single pyrenoid and urn-shaped chloroplastid, and nucleus are present. The protoplast of the cell figured as 22 contains two pyrenoids and two stigmas which indicates apparently that nuclear and cytoplasmic division are soon to follow. Unfortunately I was unable to observe division stages. Korschikoff (1925) describes reproduction as consisting of the division of the protoplast into two motile individuals which escape by the fission of the parent shell and secrete new shells for themselves.

#### SPONDYLOMORACEAE

*CHLAMYDOBOTRYS STELLATA* Korsch. (fig. 26).—As Smith (1933) points out, considerable confusion exists with reference to the occurrence of members of *Chlamydotrrys* in the United States, since they have sometimes been confused with *Spondylomorom quaternarium* which regularly has cells with four flagella. The figure of *Chlamydotrrys gracilis* reproduced as 232 by Smith (1933) and copied from an unpublished drawing of Professor Hazen, is based on material collected near London, England, so that there are, so far as I am aware, no published records of occurrence of the genus *Chlamydotrrys* in the United States except Mast's (1918) report of a biflagellated "*Spondylomorom quaternarium*." In a preliminary contribution (Bold, 1933) I reported finding *C. gracilis* Korsch. in barnyard puddles in Maryland. Subsequent observations convince me that the organism is really *C. stellata* Korsch., since it regularly occurs in the eight-celled condition and the stigmas tend to be anterior or equatorial rather than posterior. In addition the cell wall is drawn out into a distinct process posteriorly, which is typical of *C. stellata*. The cells in my specimens were about 15.4 microns in length and approximately half that width at the widest point (fig. 26).

### Explanation of Plates 6 and 7

All figures were drawn with a camera lucida and 1.9 mm. oil immersion objective, N.A. 1.30, and a 10 $\times$  compensating ocular. Figure 11 is from a stained preparation; all other figures are from living cells. The drawings are reproduced without reduction and the magnifications are as follows: Figs. 1-10 and 12 are drawn with a magnification of 1200 $\times$ ; Figure 11 approximately 1425 $\times$ ; figures 13-26 1500 $\times$ .

### Plate 6

#### *Pyramimonas montana* Geitler

- Fig. 1. Vegetative individual in surface view.
- Fig. 2. Vegetative individual in median optical section.
- Fig. 3. Anterior view of a vegetative individual.
- Fig. 4. An encysted individual.
- Figs. 5-10 and 12. Stages in asexual reproduction.
- Fig. 11. Cell fixed in corrosive sublimate and stained in Haidenhain's haematoxylin.

#### *Chlamydomonas schizochlora* Bold

- Fig. 13. Vegetative individual with stigma in surface view.
- Fig. 14. Vegetative individual in anterior view.
- Fig. 15. Vegetative individual rotated about 90°, stigma in edge view.

### Plate 7

#### *Carteria crucifera* Korsch

- Fig. 16. Vegetative individual.
- Fig. 17. Four daughter cells.

#### *Carteria ellipsoidalis* Bold

- Fig. 18. Vegetative individual in median optical section; surface view of pyrenoid.
- Fig. 19. Anterior aspect of vegetative individual.
- Fig. 20. Eight daughter cells.

#### *Chlamydomonas metastigma* (Stein) Gorosch

- Fig. 21. Vegetative individual.

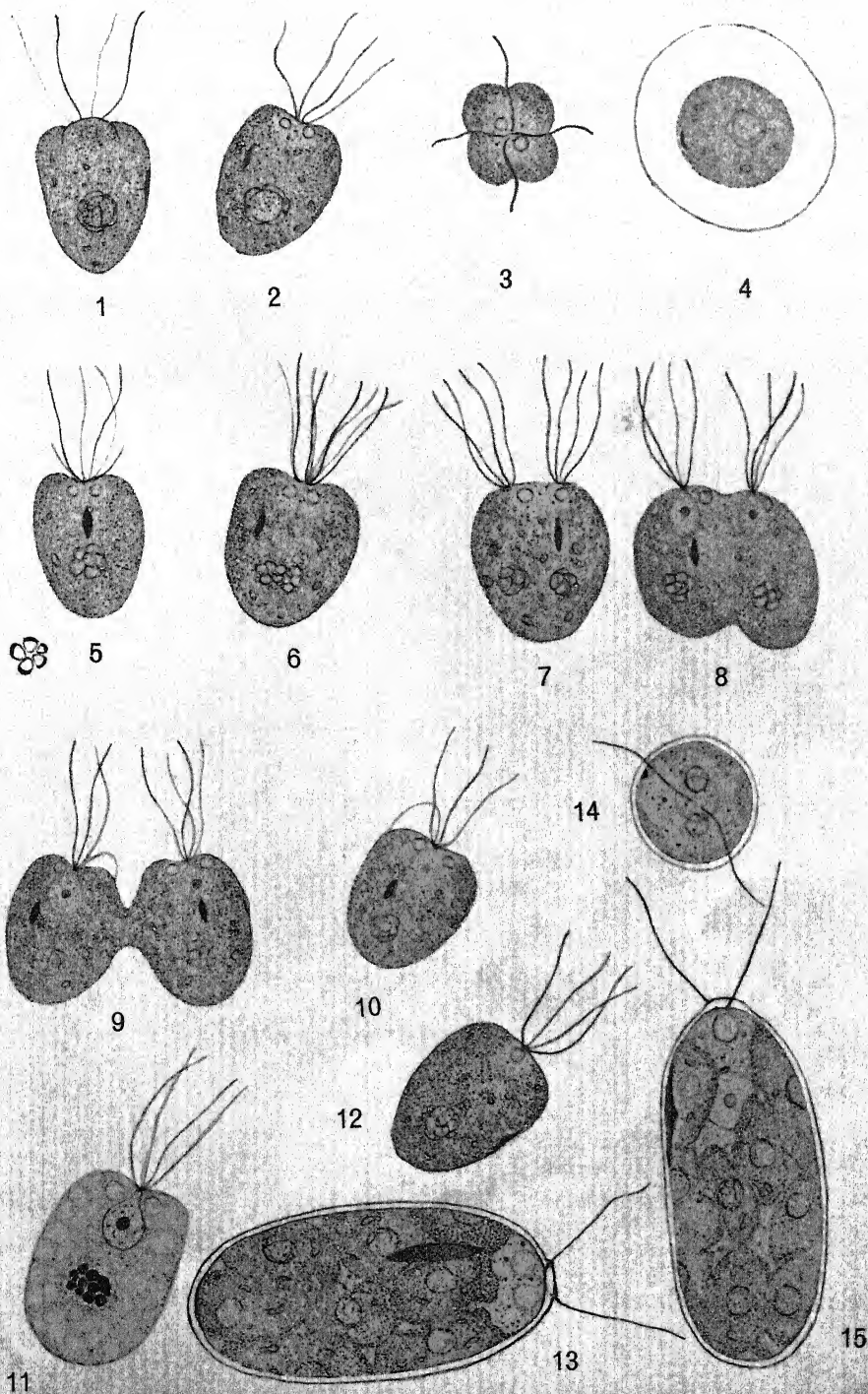
#### *Dysmorphococcus variabilis* Takeda

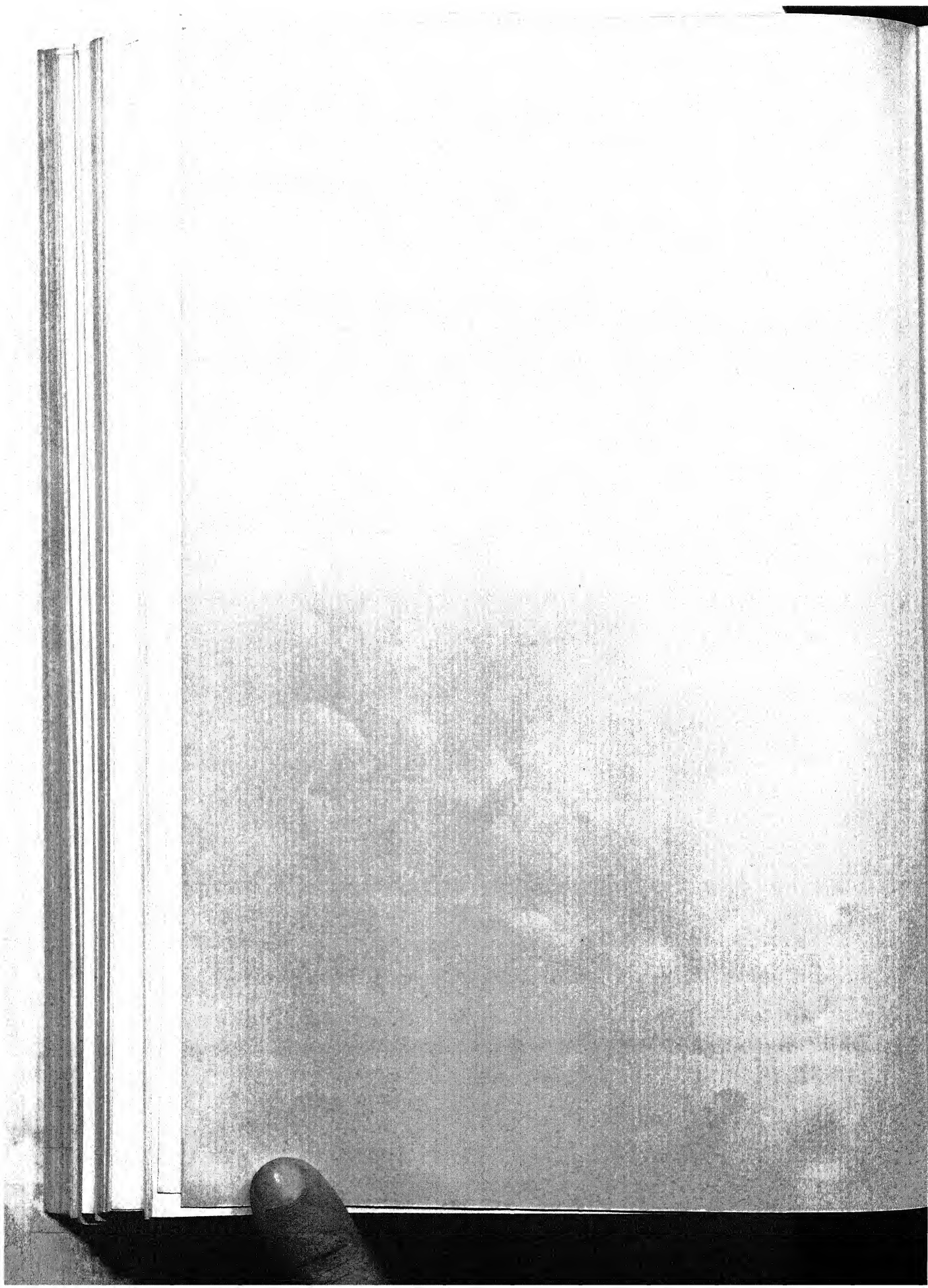
- Fig. 22. Vegetative individual preparing for division, median optical section.
- Fig. 23. Posterior view of lorica.
- Fig. 24. Anterior view of lorica showing flagellar apertures.
- Fig. 25. Surface view of a vegetative individual; detail of shell structure.

#### *Chlamydotrys stellata* Korsch.

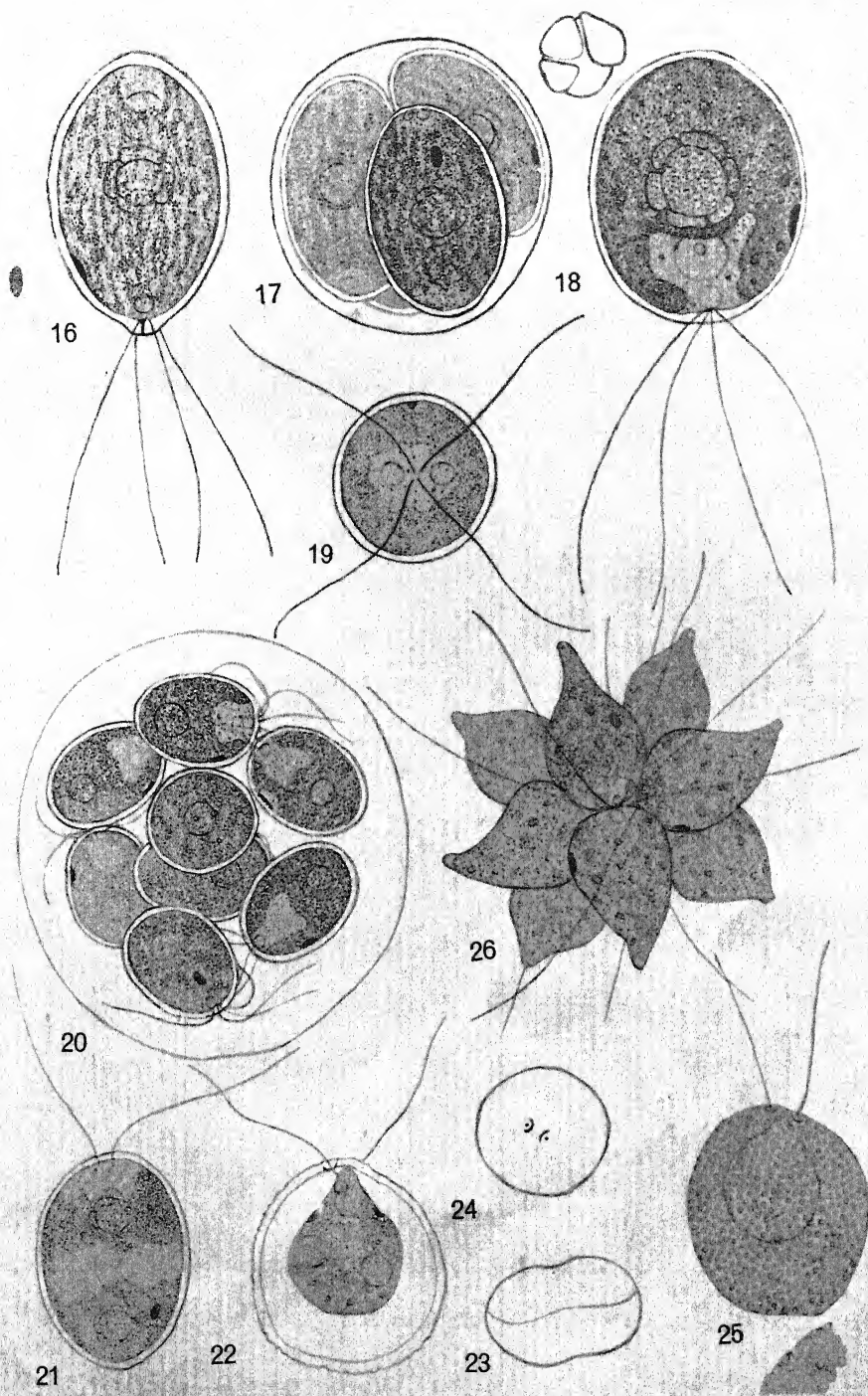
- Fig. 26. Vegetative colony.













## SUMMARY

1. Two new species, namely *Carteria ellipsoidalis* and *Chlamydomonas schizochlora* are described and figured from Maryland.

2. Five species are reported for the first time as occurring in the United States. They are: *Pyramimonas montana* Geitler, *Carteria crucifera* Korsch., *Chlamydomonas metastigma* (Stein) Gorosch., *Dysmorphococcus variabilis* Takeda, and *Chlamydotryx stellata* Korsch.

3. Asexual reproduction of *Pyramimonas montana* is described in detail.

In conclusion the author wishes to express his gratitude to Professor Tracy E. Hazen of Columbia University for criticisms and suggestions.

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## Pteridophyta of the Galapagos and Cocos Islands<sup>1</sup>

H. K. SVENSON  
(WITH PLATES 8 TO 10)

The basis for the materials of this paper is the collection made by the Astor Expedition to these islands in 1930 (specimens in herb. Brooklyn Botanic Garden), the phanerogams of which have already been reported upon.<sup>2</sup> Through the kindness of Mr. John S. L. Gilmour, now assistant director of the Royal Botanic Gardens at Kew, arrangements were made in 1933 to examine Darwin's specimens collected on the memorable voyage of the *Beagle*, now incorporated in the general herbarium of the University of Cambridge, and representing the first record of ferns from the Galapagos Islands. All of these were found with the exception of the unimportant *Asplenium subulatum*. In addition, through the kindness of Mr. Gilmour and with the help of Mr. Ballard, the collections of Captain Wood and Captain Markham, cited by Moore in *Index Filicum* and by Sir W. J. Hooker in *Species Filicum* were examined at Kew. Since genera and species have been much altered in the past century, a considerable amount of search was often necessary in locating these old specimens, but nearly all of any great interest were uncovered.

Mr. C. A. Weatherby, Senior Curator of the Gray Herbarium, has given me kindly assistance throughout my investigations. To Dr. W. R. Maxon, of the United States National Herbarium, I have been much indebted for determination of difficult species, for good advice, and for correction of occasional determinations; and to Mr. C. V. Morton of the same institution I am also indebted for help. Dr. H. A. Gleason of the New York Botanical Garden has been most kind in lending specimens from the large South American collections at that institution. Mr. John Thomas Howell of the California Academy of Sciences has most generously given me duplicates from Stewart's collection from the Galapagos Islands, and has lent me many of Stewart's critical specimens not represented in other herbaria. The abbreviations for herbaria used in the citation of specimens, I believe, are obvious.

While every effort has been made to include all important records of pteridophytes from the Galapagos Islands, thereby providing a survey of the pteridophyte flora, no such attempt is just at present being made for the ferns of Cocos Island. Despite extensive exploration, some of the ferns of Captain Wood's collection have never since been noted from the

<sup>1</sup> Brooklyn Botanic Garden Contributions. No. 83.

<sup>2</sup> Am. Journ. Bot. 22: 208-277 (1935).

Galapagos Islands, and I strongly suspect that such specimens were obtained elsewhere, probably on the continent of South America. They were undoubtedly erroneously ascribed to the Galapagos Islands through mixture of localities after the tragic death of Edmonston,<sup>3</sup> the botanist accompanying the *Pandora* (Commander, Captain Wood), which explored the Galapagos Islands in company with the *Herald*. According to Dr. Robinson (p. 221), 44 ferns were received at Kew in 1854, and the identifications by Sir W. J. Hooker were noted in scattered citations throughout *Species Filicum*. The specimens which I suspect were collected elsewhere than in the Galapagos Islands are as follows:

<i>Adiantum Alarconianum</i>	<i>Cyclopeltis semicordata</i>
" <i>patens</i>	<i>Dryopteris glandulosa</i> var. <i>brachyodus</i>
" <i>tetraphyllum</i>	" <i>rudis</i>
<i>Ananthocorus angustifolius</i>	<i>Histiopteris incisa</i>
<i>Asplenium laetum</i>	<i>Polypodium loriceum</i>
" <i>rutaceum</i>	" <i>percussum</i>
" <i>serratum</i>	<i>Pteris propinqua</i> var. <i>Cumingiana</i>

With elimination of these species, the relationships of the pteridophyte flora of the Galapagos Islands may be discussed. Since they are desert islands with moist conditions only on the windward uplands, the number of species (66) is comparatively meagre. Of the three recognized endemics, *Asplenium carolinum* is scarcely more than a form of the widespread *A. formosum*. The second, *Polypodium pleiosorus* of Darwin's collection (now to be placed in *Dryopteris*), inhabits the moist summits of James and Chatham Islands, and is close to the polymorphic West Indian and Andean *D. subincisa*. *Notholaena galapagensis*, to be described in this paper, a species of dry rocks and a relative of the Mexican *N. candida*, is perhaps the same as one or two nondescript Peruvian or Chilian collections.

Several species are of restricted range. *Polypodium tridens*, long passing under *P. squamatum*, is found also on the adjacent coast of Ecuador. *Asplenium poloense*, described from the Bolivian Andes and belonging to the difficult *lunulatum*-group, is probably more widespread than available collections indicate. Undoubtedly the most spectacular of Galapagos ferns is *Trachypteris pinnata*, a "resurrection" fern not uncommon on rocky banks, and a member of a genus with only three known species: the Galapagos plant, an inhabitant also of the Bolivian and Peruvian Andes; *T. Gillianum* from eastern Brazil and adjacent Argentina; and *T. Drake-*

<sup>3</sup> Thomas Edmonston (1825-1846), a native of the Shetland Islands, was killed by accidental gunshot on boarding a boat in the surf at Sua near Atacamas on the Ecuadorean mainland (cf. *The Phytologist* 2: 580 (1846)).



*ana*, only recently described by Christensen<sup>4</sup> from Madagascar. The remainder of the species, except for a tree-fern (*Hemitelia* aff. *subcaerulea*), a member of a group notorious for its restricted and isolated species, appear to be wide-ranging.

The following pteridophytes (40) are common to the Galapagos Islands and the West Indies:<sup>5</sup>

<i>Acrostichum aureum</i>	<i>Hypolepis repens</i>
<i>Adiantum concinnum</i>	<i>Nephrolepis biserrata</i>
" <i>macrophyllum</i>	<i>Pityrogramma calomelanos</i>
" <i>petiolatum</i>	<i>Polypodium angustifolium</i>
" <i>villosum</i>	" <i>aureum</i>
<i>Asplenium auritum</i>	" <i>crassifolium</i>
" <i>cristatum</i>	" <i>lanceolatum</i>
" <i>formosum</i> ( <i>A. carolinum</i> )	" <i>pectinatum</i>
" <i>myriophyllum</i>	" <i>Phyllitidis</i>
" <i>pumilum</i>	" <i>polypodioides</i>
" <i>Serra</i>	<i>Polystichum adiantiforme</i>
<i>Blechnum occidentale</i>	<i>Pteris biaurita</i> ( <i>P. quadriaurita</i> )
" <i>unilaterale</i>	<i>Tectaria martinicensis</i>
<i>Cheilanthes microphylla</i>	<i>Trichomanes Krausii</i>
<i>Doryopteris pedata</i>	<i>Lycopodium cernuum</i>
<i>Dryopteris gongylodes</i>	" <i>dichotomum</i>
" <i>patens</i>	" <i>reflexum</i>
" <i>Poiteana</i>	" <i>taxifolium</i>
" <i>tetragona</i>	<i>Psilotum nudum</i>
<i>Elaphoglossum petiolatum</i>	
<i>Hymenophyllum ciliatum</i>	

Cocos Island (off the coast of Costa Rica) and the Galapagos Islands have a number of pteridophytes in common. Though only three miles in diameter, Cocos has a high proportion of ferns (22 species were collected by the Astor Expedition), due to the heavy covering of tropical rain forest. The following species (8) are found on both the Galapagos and Cocos Islands.

<i>Acrostichum aureum</i>	<i>Pityrogramma calomelanos</i>
<i>Adiantum petiolatum</i>	<i>Polypodium aureum</i>
<i>Nephrolepis biserrata</i>	" <i>Phyllitidis</i>
" <i>pectinata</i>	<i>Polystichum adiantiforme</i>

Several widely distributed tropical pteridophytes (19) are known from the Galapagos Islands and Madagascar (cf. Christensen, l.c.):

<sup>4</sup> Dansk Bot. Arkiv 7: 111. t. 42 (1932).

<sup>5</sup> Cf. Domin, The Pteridophyta of Dominica, Roy. Czech. Soc. Nat. Hist. Mém. n. ser. no. 2 (1929); Maxon, Surv. Porto Rico and Virgin Ids. 6: 373-521 (1926).

*Acrostichum aureum*  
*Anogramma leptophylla*  
*Asplenium auritum*  
 " *formosum* (*A. carolinum*)  
 " *praemorsum*  
*Dryopteris gongylodes*  
 " *mollis*  
*Elaphoglossum petiolatum*  
*Gleichenia linearis*  
*Hymenophyllum ciliatum*

*Nephrolepis biserrata*  
*Pityrogramma calomelanos*  
*Polypodium lanceolatum*  
*Polystichum adiantiforme*  
*Pteris quadriaurita* (*P. biaurita*)  
*Lycopodium cernuum*  
 " *clavatum*  
 " *complanatum*  
*Psilotum nudum*

In the Galapagos Archipelago, the distribution of ferns is probably much the same on all the larger islands. As is the case with the flowering plants of Indefatigable Island,<sup>6</sup> different species of ferns are progressively seen as one ascends the moist mountain slopes from the desert areas of the coast, and a similar progression probably occurs on the windward side of all the larger islands. At Academy Bay, on the south (and moist) side of Indefatigable Island the first fern to be encountered is *Notholaena galapagensis*, which is abundant on the escarpment at about 100 ft. elevation. Exposed lava banks soon reveal the rosettes of *Trachypteris pinnata*, a species which reaches its maximum development on rocks and logs in the damper woodlands. At about 500 ft. *Asplenium auritum* and *Polypodium lepidopteris* cluster on tree trunks with *Tillandsia insularis* and the orchid, *Ionopsis utricularioides*. At this elevation, by brushing aside grasses and shrubbery, one can readily disclose *Doryopteris pedata*, *Asplenium carolinum*, and *Polypodium tridens* beneath the shade of jagged lava fragments. When the densest vegetation is reached, at about 800 ft., bird's-nest ferns (*Polypodium Phyllitidis*) and maidenhair ferns (*Adiantum Henslovianum*) are not uncommon in the underbrush. A little higher, in the cleared areas of the plantation *Fortuna*, a strong growth of *Hypolepis repens* and occasional plants of *Adiantum villosum* are encountered, perhaps owing their presence to human habitations. On the steep mountain slope above the plantation, overhanging boulders provide shaded spots suitable for the growth of *Adiantum macrophyllum*, and for the yellow-powdered fronds of *Gymnogramme tartarea*. Toward the summit, at an altitude of about 2,000 ft.—the highest point our party was able to reach—the dwarfed trees are festooned with liverworts and epiphytic lycopodiums, on the ground there are banks of *Blechnum unilaterale* and *Nephrolepis pectinata*, and in openings tall brakes of *Pteridium arachnoideum* are not uncommon.

<sup>6</sup> Cf. Tabular view of Altitudinal Distribution, *Am. Journ. Bot.* 22: 210-211 (1935).

Bibliographical references occurring frequently in the text are abbreviated as follows:

Rob. (1). Robinson, B. L. Flora of the Galapagos Islands. Proc. Amer. Acad. 38: 77-269, 3 pl. (1902).

Stewart (1). Stewart, A. A botanical survey of the Galapagos Islands. Proc. California Acad., ser. 4, 1: 7-288, 19 pl. (1911).

Stewart (2). Stewart, A. Notes on the botany of Cocos Island. Proc. California Acad., ser. 4, 1: 375-404, 4 pl. (1912).

The collections by Rorud were cited in E. Christophersen, *Nyt. Mag. for Naturvidenskaberne* 70: 69-70 (1932), and were determined by Dr. Christensen. Moore's references to Galapagos ferns and early citations by Andersson, Caruel, etc. will be found in Dr. Robinson's account.

#### FILICES<sup>7</sup>

##### ACROSTICHUM L.

*A. AUREUM* L. Sp. Pl. 1069 (1753); Rob. (1), 104; Stewart (1), 11.—ALBEMARLE ISL.: Villamil, 3150 ft., *Stewart*. GALAPAGOS IDS.: *Capt. Wood*, two sheets of rather young material.

##### ADIANTUM L.

\**A. ALARCONIANUM* Gaud. Voy. Bon. Bot. t. 99 (1846); Stewart (1), 11. *A. incisum* Presl; Rob. (1), 105.—GALAPAGOS IDS.: *Capt. Wood*, two sheets of branched specimens (as *A. incisum* Presl).

*A. CONCINNUM* H. & B. in Willd. Sp. 5: 451 (1810); Rob. (1), 105; Stewart (1), 11. *A. cuneatum* sensu Hook.f. Trans. Linn. Soc. 20: 168 (1847), not Langsd. & Fisch. *A. aethiopicum* sensu Moore, Ind. Fil. 19: (1857), not L.; Rob. (1), 105; Stewart (1), 11.—ABINGDON ISL.: *Snodgrass & Heller*; *Stewart*. ALBEMARLE ISL.: *Snodgrass & Heller*; *Stewart*. CHARLES ISL.: *Stewart*. INDEFATIGABLE ISL.: *Rorud*. JAMES ISL.: *Darwin*; *Scouler*; *Snodgrass & Heller*. NARBOROUGH ISL.: *Snodgrass & Heller* (?). GALAPAGOS IDS.: *Douglas* (Kew).

Darwin's collection is typical *A. concinnum*. The specimen of *A. aethiopicum*, collected by Douglas, and evidently the basis of Moore's citation, is without question a small, poor specimen of the same species. It has a perfectly smooth rachis and a few very old sori.

*A. HENSLOVIANUM* Hook.f. Trans. Linn. Soc. 20: 169 (1847); Rob. (1), 105; Stewart (1), 11. *A. parvulum* Hook.f. Trans. Linn. Soc. 20: 168 (1847). *A. diaphanum* sensu Stewart (1), 11; not Bl.—ABINGDON ISL.: *Stewart*. ALBEMARLE ISL.: *Stewart*, including no. 785 (Cal) (as *A. diaphanum*).

<sup>7</sup> Species marked by an asterisk (\*) are probably not from the Galapagos Islands. Previous inclusion in the flora is probably due to Edmonston's confused data. (See introduction, p. 304.)

CHARLES ISL.: *Darwin* (4 specimens). CHATHAM ISL.: *Baur*; *Stewart* no. 784 (US) (as *A. concinnum*). INDEFATIGABLE ISL.: *Stewart*; Academy Bay, wet shady places among rocks, 1100–1500 ft., *Svenson* no. 144. JAMES ISL.: *Darwin*; *Stewart*.

*Darwin*'s specimen of *Adiantum parvulum* (from Charles Island) is a very small example with pinnules not exceeding 10 mm.  $\times$  4 mm. and none have more than one or two sori. The shiny, almost black stipe has somewhat clavate scurf, exactly as in *A. Henslovianum*. The material reported by *Stewart* as *Adiantum diaphanum* is very young but shows under microscopic examination the indusia characteristic of *A. Henslovianum*, and the same type of scurfy rachis.

A. MACROPHYLLUM Sw. Prod. 135 (1788); *Stewart* (1), 12.—ALBEMARLE ISL.: *Stewart*. INDEFATIGABLE ISL.: *Stewart*; *Rorud*. JAMES ISL.: *Stewart*. Young fronds of this species, of a translucent, pinkish color, were noted but not collected, beneath damp boulders at about 1,000 ft. elevation at Academy Bay.

\*A. PATENS Willd. Sp. 5: 439 (1810); *Stewart* (1), 12.—GALAPAGOS IDS.: *Capt. Wood*. The specimen which I saw at Kew is identical with *Schlim* no. 616 from Ocaña, New Granada, and very close to *Seeman* no. 1448 from Mexico.

A. PETIOLATUM Desv. Berl. Mag. 5: 326 (1811); *Stewart* (1), 12. *A. Kaulfussii* Kunze, Linnaea 21: 221 (1848); Rob. (1), 105.—CHATHAM ISL.: *Capt. Wood* (Kew), a specimen of apparently typical material.

\*A. TETRAPHYLLUM H. & B. in Willd. Sp. 5: 441 (1810); *Stewart* (1), 12. *A. prionophyllum* HBK Nov. Gen. & Sp. 1: 20 (1815); Rob. (1) 106.—CHATHAM ISL.: *Capt. Wood*, two sheets identical with *Lehmann* no. 7685.

A. VILLOSUM L. Syst. Nat. ed. 10, 2: 1328 (1759).—INDEFATIGABLE ISL.: Academy Bay, in cut-over places in vicinity of the Plantation Fortuna, 800 ft., *Svenson* no. 101; Academy Bay, 500 ft., *Stewart* no. 798 (G) (as *E. petiolatum*). My collection is in excellent agreement with *Schkuhr*'s plate.

#### ANOGRAMMA Link

A. CHAEROPHYLLA (Desv.) Link, Fil. Sp. 138; (1841) *Stewart* (1), 12. *Gymnogramma chaerophylla* Desv. Berl. Mag. 5: 305 (1811); Rob. (1), 109.—CHARLES ISL.: *Darwin*, the specimen is in good condition and unquestionably *A. chaerophylla*.

A. LEPTOPHYLLA (L.) Link, Fil. Sp. 137 (1841); *Stewart* (1), 12. *Gymnogramma leptophylla* Desv. Berl. Mag. 5: 305 (1811); Rob. (1), 109.—CHARLES ISL.: *Baur*.

## ANANTHOCORUS Underw. &amp; Maxon

\**A. ANGUSTIFOLIUS* (Sw.) Underw. & Maxon, Contr. U. S. Nat. Herb. 10: 487 (1908). *Vittaria angustifolia* (Sw.) Bak. Fl. Bras. 1<sup>2</sup>: 544 (1870); Stewart (1), 27. *Pteris angustifolia* Sw. Prod. 129 (1788). *Taenitis angustifolia* Spr. Syst. 4: 42 (1827); Hook. Sp. Fil. 5: 187 (1864); Rob. (1), 115.—GALAPAGOS IDS.: Capt. Wood, the specimen (cited by Hooker) has fronds 3 dm. long, and as much as 8 mm. wide.

## ASPLENIUM L.

*A. AURITUM* Sw. in Schrad. Journ. 1800<sup>2</sup>: 52 (1801); C. Chr. Archiv. f. Bot. 9<sup>II</sup>: 16, t. 1, fig. 1 (1910); Rob. (1), 106; Maxon, Bot. Porto Rico & Virgin Ids. 6: 450 (1926); Domin, Pterid. Dominica 176 (1929). *A. sulcatum* Lam. Encyc. 2: 308 (1786); Stewart (1), 15. *A. marinum* var. *auriculatum* Hook.f. Trans. Linn. Soc. 20: 170 (1847). *A. auritum* var. *macilentum* Moore, Ind. Fil. 115 (1859); Rob. (1), 107. *A. lunulatum* sensu Rob. (1) 107; not Sw.—ABINGDON ISL.: Snodgrass & Heller; Stewart. ALBEMARLE ISL.: Stewart. CHARLES ISL.: Darwin; Andersson; Agassiz; Stewart. CHATHAM ISL.: Capt. Wood; Stewart. INDEFATIGABLE ISL.: Stewart; Svenson. JAMES ISL.: Darwin; Stewart; Rorud (var. *macilentum*).

Much variation is shown in Captain Wood's collection at Kew. One of his specimens (Chatham Isl.) with somewhat dissected pinnae and the accompanying query "rigidum?" strongly resembles Stewart's no. 812 (James Isl.) but is far removed from *A. rigidum* as illustrated by Christensen (l.c.). The third collection, labeled merely "Galapagos Islands," is a small var. *macilentum* with small obtuse pinnae and no trace of auricles.

Domin (l.c.) notes that var. *macilentum* is abundant in Jamaica at an altitude of from 5,000 to 6,000 ft. on exposed rocks. From personal observation I cannot see that the variations displayed in the Galapagos Islands are significant from the point of view of geographical distribution. Of the three collections of this abundant epiphyte which I made on Indefatigable Island, no. 53 (500 ft. altitude) verges toward var. *macilentum*; no. 100 (700 ft.) is nearer the type; and no. 97 (2,000 ft.) is var. *macilentum*. The specimens cited by Christophersen, determined by Christensen as "var. *macilentum*" came two kilometers from the shore, on James Island. None of the specimens which I have seen are characterized by a "rachis broadly winged," stated by Hooker & Baker (Syn. Fil. 208 (1873)) as one of the characteristics of *A. macilentum*.

Lee's specimens of *A. lunulatum* (U. S. Nat. Herb.) are, according to a communication from Dr. Maxon, representative specimens of *A. auritum*. Darwin's collections are of the typical form.



*A. FORMOSUM* Willd. Sp. 5: 329 (1810); Rob. (1), 107; Stewart (1), 13. *A. carolinum* Maxon, Contr. U. S. Nat. Herb. 17: 148 (1913). *A. subulatum* Hook. & Arn. Bot. Beech. Voy. 312, t. 71 (1840); Hook.f. Trans. Linn. Soc. 20: 169 (1847) (as *A. subulatum*); Andersson, [Eugenies Resa, Bot.] Kgl. Sv. Vet. Akad. Handl. 1853: 131 (1854) and 1857: 41 (1861).—ABINGDON ISL.: Snodgrass & Heller; Stewart. ALBEMARLE ISL.: Snodgrass & Heller; Stewart. CHARLES ISL.: Darwin; Capt. Markham (Kew), labeled "11-80"; Lee; Baur; Stewart. CHATHAM ISL.: Capt. Wood; Cuming (Kew); Stewart. INDEFATIGABLE ISL.: Stewart; Rorud; Academy Bay, common in leaf mould in rocky woods, 500 ft., Svenson no. 75. JAMES ISL.: Stewart. NARBOROUGH ISL.: Stewart.

"*Asplenium subulatum*" Hook.f. was the only specimen of the Darwin collection which I was unable to find at Cambridge.

*A. CRISTATUM* Lam. Encyc. 2: 310 (1786); Stewart (1), 13. *A. cicutarium* Sw. Prod. 130 (1788). *A. rhizophyllum* sensu Rob. (1), 107, not Kunze. *A. Macraei* sensu Hook.f. Trans. Linn. Soc. 20: 169 (1847), not Hook. & Grev. *A. myriophyllum* sensu Stewart (1), 14, not (Sw.) Presl.—ABINGDON ISL.: Stewart. ALBEMARLE ISL.: Stewart. CHATHAM ISL.: Capt. Wood; Baur; Stewart. INDEFATIGABLE ISL.: Stewart; Rorud; Academy Bay, common among rocks in shade of shrubs and vines, 800 ft., Svenson no. 108. JAMES ISL.: Darwin; Stewart.

Identity of the Galapagos plants has been greatly confused due to merging of the perfectly distinct *A. Macraei* of the Hawaiian Islands and Cocos Island with *A. rhizophyllum*, and confusion of *A. cristatum* (*A. cicutarium*) of the Galapagos Islands with *A. rhizophyllum*.

Two specimens of *A. cristatum* at Kew were collected on Chatham Island by Captain Wood. One of these is labeled *A. rhizophyllum*, (a distorted specimen partially covered with liverworts and mounted with Jameson no. 28 from Quito); the other is labeled *A. Macraei* and mounted on a sheet of that species. Darwin's collection at Cambridge (consisting of two sheets labeled *A. Macraei*) is also *A. cristatum*. These collections of Darwin and Capt. Wood are the only basis for Stewart's citation of *A. myriophyllum*.

\**A. LAETUM* Sw. Syn. Fil. 79, 271 (1806); Rob. (1), 107; Stewart (1), 14.—CHATHAM ISL.: Capt. Wood. This specimen, the only record for the Galapagos Islands, has pinnae 2.5–3 cm. long and 0.8–1.0 cm. broad, the margin sharply but somewhat irregularly serrate. The species is abundant in the West Indies (cf. Domin, Pter. Dominica 174, (1929)), and in continental America extends from Mexico to Southern Brazil.

*A. MYRIOPHYLLUM* (Sw.) Presl, Rel. Haenk. 1: 48 (1825).—INDEFATIGABLE ISL.: In the forest, the moist region, 255–300 m., Rorud no. 254.



(Specimen (det. Christensen) examined through the kindness of Dr. Erling Christophersen).

A. POLOENSE Rosenst. in Fedde, Rep. Spec. Nov. 12: 469 (1913).—INDEFATIGABLE ISL.: Academy Bay, south slope of the mountain on vertical damp ledges in stream bed, 1000–5000 ft., *Svenson* no. 130. The rachis is slightly channeled and compressed-sulcate at base; the shiny subulate scales are deep brown with clearly-defined reticulation at the apex. *A. poloense* is a Bolivian species known previously only from Buchtien's no. 3345, collected in "Yungas septentrionalis, Polo-Polo prope Coroico, 900 m. alt." It is said to be related to *A. pulcherrima* Raddi (? *A. pulchellum*) and in its strongly auriculate and deeply incised pinnae it approaches *A. Fernandezianum* Kze.

A. PRAEMORSUM Sw. Prod. 130 (1788); Stewart (1), 14. *A. furcatum* Thunb. Prod. Fl. Cap. 172 (1800); Hook.f. Trans. Linn. Soc. 20: 169 (1847); Rob. (1), 107.—ALBERMARLE ISL.: *Snodgrass & Heller*; Stewart. JAMES ISL.: *Darwin*; Stewart. NARBOROUGH ISL.: Stewart. INDEFATIGABLE ISL.: Stewart; Academy Bay, a common epiphyte at 1,400–1,500 ft. *Svenson* no. 128, and 2,000 ft. (no. 211). I did not see Capt. Wood's collection cited by Hooker, Sp. Fil. 3: 167 (1860). A species of wide tropical distribution.

A. PUMILUM Sw. Prod. 129 (1788); Stewart (1), 14.—CHARLES ISL.: Stewart. INDEFATIGABLE ISL.: Stewart. Stewart's collections closely resemble Small's illustration in Ferns of Florida: 133 (1931).

\*A. RUTACEUM (Willd.) Metten. Abh. Senck. Nat. Gesell. Frankfurt 3: 129, t. 5, fig. 32–33 (1859); Rob. (1), 108; Stewart (1), 14.—CHATHAM ISL.: *Capt. Wood*. The specimen is identical with *Moritz* no. 402 from Tovar Colombia (K).

A. SANGUINOLENTUM Kunze ex Mett. Abh. Senck. Nat. Gesell. Frankfurt 3: 142, t. 4, fig. 10 (1859). *A. nigrescens* Hook.f. Trans. Linn. Soc. 20: 170 (1847), not Blume (1828). *A. nubilum* Moore<sup>8</sup> Ind. Fil. 150 (1859). *A. anisophyllum* var. *latifolium* Hook.f., Sp. Fil. 3: 111 (1860); Rob. (1), 106; Stewart (1), 13. *A. sarcodes* Maxon, Contr. U. S. Nat. Herb. 10: 494, t. 56, fig. 3 (1908). *A. anisophyllum* var. *sanguinolentum* Hieron. Hedwigia 47: 226 (1908).—ALBEMARLE ISL.: *Capt. Wood*; Stewart no. 857 (G), (as *A. Serra*). CHATHAM ISL.: Stewart no. 858 (G, Cal, NY) (as *A. Serra*). INDEFATIGABLE ISL.: Academy Bay, 1000–1600 ft., plants 3 ft. high with a prominent blackened base, *Svenson* nos. 125, 221. JAMES ISL.: *Darwin*; above 2000 ft., Stewart nos. 860 (Cal), 861 (Cal, G) (as *A. Serra*).

<sup>8</sup> Moore's name appeared in December, 1859. Maxon (l.c.) gives the year, 1860, for Mettenius' publication, but in a later treatment (Bot. Porto Rico & Virgin Isls. 6<sup>3</sup>: 449 (1926)), the date appears as 1859, which would undoubtedly be earlier than the issue of Moore's name.

The two sheets of Darwin's collection (upon which the name *A. nubilum* was based) are substantially the same as mine and identical with material from Cuba, and with Maxon's figure of *A. sarcodes*. The latter species has already been placed in synonymy under the wide-spread *A. sanguinolentum* by Christensen.

\**A. Serra* Langsd. & Fisch. Icon. Fil. 16, t. 19 (1810); Rob. (1), 108; Stewart (1), 15.—ALBEMARLE ISL.: *Stewart* nos. 856, 857 (Cal). DUNCAN ISL.: *Stewart* no. 859 (Cal). GALAPAGOS IDS.: *Capt. Wood*; no definite locality is given on the label.

*A. SERRATUM* L. Sp. Pl. 1079 (1753); Rob. (1), 108; Stewart (1), 15.—CHATHAM ISL.: *Capt. Wood*. The specimen at Kew is representative of this large bird's-nest fern.

#### BLECHNUM L.

*B. OCCIDENTALE* L. Sp. Pl. 1077 (1753); Rob. (1), 108; Stewart (1), 16.—ABINGDON ISL.: *Snodgrass & Heller; Stewart*. ALBEMARLE ISL.: *Snodgrass & Heller; Stewart*. CHARLES ISL.: *Andersson; Stewart*. CHATHAM ISL.: *Chierchia; Baur*. DUNCAN ISL.: *Stewart*. JAMES ISL.: *Darwin; Stewart*. Darwin's specimen is typical. *Capt. Wood's* collection, cited as var. *caudatum* by Hooker (Sp. Fil. 3: 51 (1860)) consists of two specimens neither of which is labeled as the variety. One is a loose poorly-dried plant, with pinnae up to 10 cm. long and 12 mm. wide; the other has pinnae 2–3 cm. long, 5 mm. wide.

*B. UNILATERALE* Sw. Berl. Mag. 4: 79, t. 3, fig. 1 (1810); Maxon, Bot. Porto Rico & Virgin Isl. 6<sup>3</sup>: 456 (1926). *B. blechnoides* (Lag.) C. Chr. Ind. 151 (1905); Stewart (1), 15.—CHATHAM ISL.: Wreck Bay, 1700–2000 ft., *Stewart*. INDEFATIGABLE ISL.: Academy Bay, and epiphyte on the south slope of the mountain, alt. 2000 ft., *Svenson* no. 148, and not uncommon on the ground, alt. 2000 ft., *Svenson* no. 210.

#### CHEILANTHES Sw.

*C. MICROPHYLLA* Sw. Syn. 127 (1806); Rob. (1), 108; Stewart (1), 16; Maxon, Contr. U. S. Nat. Herb. 24: 52 (1922). *C. heterotricha* Andersson, [Eugenies Resa Bot.] Sv. Vet. Akad. Handl. 1853: 129 (1854).—ABINGDON ISL.: *Stewart*. ALBEMARLE ISL.: *Snodgrass & Heller*; shady place near shore, *Stewart*. CHARLES ISL.: *Andersson; Stewart*. CHATHAM ISL.: *Baur*. INDEFATIGABLE ISL.: *Stewart*; Academy Bay, dry places along trails, 300 ft., *Svenson* no. 256. GALAPAGOS IDS.: *Capt. Wood* (Kew), a specimen labeled "Pellaea?", identical with *Stewart* no. 875 (Kew) from Albemarle Island.

*C. MYRIOPHYLLA* Desv. Berl. Mag. 5: 328 (1811); Rob. (1), 109; Stewart (1), 17.—ALBEMARLE ISL.: *Snodgrass & Heller*.

## CYCLOPELTIS J. Sm.

\*C. SEMICORDATA (Sw.) J. Sm. in Curtis, Bot. Mag. 72: Comp. 36 (1846); Stewart (1), 17. *Aspidium semicordatum* Sw.; Rob. (1), 106.— GALAPAGOS IDS.: Capt. Wood (Kew); two sheets.

## DENNSTAEDTIA Bernh.

D. aff. GLOBULIFERA (Poir.) Hieron. in Engler, Bot. Jahrb. 34: 455 (1904). *Polystichum apiifolium* sensu Stewart (1), 26; not (Sw.) C. Chr.— JAMES ISL.: occasional at 2000 ft. Stewart nos. 882, 883.

## DICRANOPTERIS Bernh.

D. LINEARIS (Burm.) Underwood, Bull. Torrey Club 34: 250 (1907). *Gleichenia linearis* (Burm.) Clarke, Trans. Linn. Soc. 2: Bot. 1: 428 (1880); Stewart (1), 20. *G. dichotoma* Hook. Sp. Fil. 1: 12 (1846); Rob. (1), 109.— CHATHAM ISL.: Stewart. DUNCAN ISL.: Stewart. GALAPAGOS IDS.: Capt. Wood. This collection, probably representing the citation by Moore (Ind. Fil. 376 (1862)), is the same as Stewart's collections, but a larger specimen. The exact identity of this material is uncertain.

## DIPLAZIUM Sw.

D. aff. SUBOBTUSUM Rosenstock in Fedde, Rep. Spec. Nov. 7: 296 (1909).—INDEFATIGABLE ISL.: Academy Bay, plants 4–5 ft. high, alt. 1625 ft., south slope of the mountain (Svenson no. 132) (Pl. 9, fig. 3). The segments are less acute than in *D. subobtusum*, which was described from a collection by Spruce (no. 4019) from Mt. Guayrapurina, Ecuador. It is related to *D. obtusum* Desv.

## DORYOPTERIS J. Sm.

D. PEDATA (L.) Fée, Gen. Fil. 133 (1852); Stewart (1), 18. *Pteris pedata* L. Sp. Pl. 1075 (1753); Rob. (1), 114. *Litobrochia pedata* Presl; Hook. f. Trans. Linn. Soc. 20: 168 (1847).—ABINGDON ISL.: Stewart. ALBEMARLE ISL.: Snodgrass & Heller; Stewart. CHARLES ISL.: Darwin; Andersson; Capt. Markham; Lee; Baur; Stewart. CHATHAM ISL.: Baur; Stewart. INDEFATIGABLE ISL.: Stewart; Rorud; Academy Bay, abundant in damp places among rocks, alt. 400 ft., Svenson no. 69. JAMES ISL.: Darwin; Douglas; Cuming; Stewart.

The collection by Darwin from James Island represents young material without sori; that from Charles Island is mature. I have also seen the specimens obtained by Capt. Wood, Cuming, and Capt. Markham, but was unable to locate any specimen of *Doryopteris concolor* (Pellaea ge-

*raniaefolia*) cited by Hooker, Sp. Fil. 2: 133 (1858), nor did I find either at Cambridge or Kew any collection of *D. pedata* by Douglas. Since *D. concolor* (coll. Douglas) has never reappeared in any collection from the Galapagos Islands, it is probable that the specimen was confused with the similar *D. pedata*, or came from some other locality.

DRYOPTERIS Adans.

*D. AMPLA* (Willd.) O. Ktze. Rev. Gen. Pl. 2: 812 (1891); C. Chr. Vid. Selsk. Skr. ser. 8, 6<sup>1</sup>: 49, fig. 9 (1920). *Polypodium paleaceum* Hook.f. Trans. Linn. Soc. 20: 166 (1847); Andersson, [Eugenies Resa Bot.] Sv. Vet. Akad. Handl. 1853: 126 (1854); Robinson (1), 112. *Nephrodium paleaceum* (Hook.f.) Diels, Nat. Pfl. 1<sup>4</sup>: 177 (1899). *Dryopteris furcata* (Kl.) O. Ktze. Rev. Gen. 2: 812 (1891); Stewart (1), 18.—ALBEMARLE ISL.: Iguana Cove, *Snodgrass & Heller* no. 113 (G); lava caverns, Villamil, 1350 ft., *Stewart* no. 959 (NY); upper regions, Villamil, *Stewart* no. 965 (NY). CHARLES ISL.: *Darwin*; summit of the mountain, *Andersson* (G); Lee (US); *Stewart*. CHATHAM ISL.: southwest end, middle region, *Baur* no. 367 (G), (as *Alsophila* sp.); Wreck Bay, 650 ft., *Stewart* no. 960 (G). INDEFATIGABLE ISL.: *Rorud*; Academy Bay, 550 ft., *Stewart* no. 963 (G); Academy Bay, at the Plantation Fortuna, 800 ft., *Svenson* nos. 105, 106. JAMES ISL.: *Darwin*; James Bay, 2750 ft., *Stewart* no. 962 (G, NY).

Darwin's collections are represented by two sheets; the specimens of Capt. Wood and Capt. Markham at Kew (without further locality) are poorly prepared, but unquestionably the same. *D. ampla*, according to Christensen (l.c.), is known from "the northern Andes of Venezuela, Colombia and Ecuador to Costa Rica and Guatemala, Jamaica and Cuba, from where it has found its way to Florida, and the southern Lesser Antilles from Trinidad to St. Vincent."

*D. COLUMBIANA* C. Chr. Vid. Selsk. Skr. 7<sup>4</sup>: 279, fig. 8 (1907); Vid. Selsk. Skr. 10<sup>2</sup>: 137 (1913).—INDEFATIGABLE ISL.: Academy Bay, damp openings at 1500 to 2000 ft., *Svenson* nos. 216 and 219. CHARLES ISL.: *Stewart* no. 909 (G) (as *D. parasitica*). CHATHAM ISL.: *Capt. Wood* (an unidentified specimen at Kew). Further distribution: Colombia, Panama.

The material which I have cited under this name is not exactly homogeneous, and it would perhaps be as well to have called it *D. pilosula* (Kl. et Karst.) Hieron. In fact it combines the characteristics of these two species as they are treated by Christensen, who was not at all times certain of their specific distinction. These terrestrial ferns of the *Lastraea* group do not appear to be abundant in the Galapagos Islands, being confined apparently to the moist, windward slopes of the mountains. However, I noted that they occurred fairly commonly from 1500 ft. to 2000 ft. eleva-

tion on Indefatigable Island, the fronds of specimens (no. 219) collected at the lower elevation being comparatively thin, and with the short rachis-pubescent of *D. columbiana*. The collection from 2000 ft. (no. 216), on the other hand, had distinctly coriaceous fronds, and the longer rachis-pubescent of *D. pilosula*. But the two types of rachis-pubescent often vary in fronds of the same clump, and indeed, in different portions of the same frond. The development of leathery texture is undoubtedly associated with the rapidly dwarfing character of the vegetation as one approaches the mountain-summits, and this leathery texture is probably correlated to Christensen's characterization of *Dryopteris ampla* as found in the Galapagos Islands (1920, p. 52), "At best it is a dwarfy form developed in exposed localities on the high mountains of the islands." Capt. Wood's collection closely resembles my no. 219.

The characteristic rigid hairs of *D. columbiana*, on the veins of the upper segment surface, are not particularly well developed in the Galapagos specimens (more developed in no. 216 than in no. 219), which tend also to be more pubescent than in the type collection of *D. columbiana* (NY). The apical portions of young fronds in the Galapagos specimens show very well the character of the indusium, which is reniform to ovate. The indusial hairs (5-9) are all marginal, except that a single one is frequently present in no. 216 at the upper surface, at the point of attachment of the indusium. The character of the indusium agrees, so far as I can make out with the type collection of *D. columbiana*, and not with *D. pilosula*, which tends to have a number of hairs on the upper indusial surface. The margin of the indusium is quickly folded up by the developing sporangia, and soon buried among the mature sporangia, so that the sorus often appears to be non-indusiate.

\**D. GLANDULOSA* (Desv.) C. Chr. var. *BRACHYODUS* (Kunze) C. Chr. Vid. Selsk. Skr. ser. 7, 10<sup>2</sup>: 172 (1913). *D. brachyodus* (Kze.) O. Ktze. Rev. Gen. Pl. 2: 812 (1891); Stewart (1), 18. *Nephrodium brachyodon* Hook. Sp. Fil. 4: 83 (1862); Rob. (1), 110.—Known only from the collection by Capt. Wood (Kew), where no further locality is given. Specimens are cited by Christensen from Guatemala to Colombia; the type coming from Pompayaco, Peru.

*D. GONGYLODES* (Schkuhr) O. Ktze. Rev. Gen. Pl. 2: 811 (1891); C. Chr. Vid. Selsk. Skr. ser. 7, 10<sup>2</sup>: 193 (1913). *Nephrodium unitum* R. Br.; Rob. (1), 110.

Listed by Dr. Robinson on the strength of Caruel's determination of Chiercha's collection. The species is close to *D. mollis*, and the Galapagos specimen probably represents either that species or *D. columbiana*.

*D. dentata* (Forsk.) C. Chr. Vid. Selsk. Skr. ser. 8, 6<sup>1</sup>: 24 (1920). *D.*



*mollis* (Jacq.) Hieron. Hedwigia 46: 348 (1907); C. Chr. Vid. Selsk. Skr. ser. 7, 10<sup>2</sup>: 191 (1913).—JAMES ISL.: Stewart no. 915 (G) (as *D. tricholepis*), and perhaps some of his collections listed under *D. parasitica*. Lee's collection from Charles Island is doubtfully placed under *D. mollis* by Christensen (1913). By the same author (Dansk Bot. Arkiv. 7: 49 (1932)), and by Maxon, Bot. Porto Rico and Virgin Ids. 6<sup>3</sup>: 470 (1926), *D. mollis* is treated as a synonym of *D. dentata* (Forsk.) C. Chr.

D. PATENS (Sw). O. Ktze., Rev. Gen. Pl. 2: 813 (1891); C. Chr. Ark. f. Bot. 9<sup>11</sup>: 28, fig. 6 (1910) and Vid. Selsk. Skr. ser. 7, 10<sup>2</sup>: 176 (1913). *Nephrodium molle* Schott, sensu Hook.f. (1), 171 (1847); Rob. (1), 110. *Dryopteris parasitica* (L.) O. Ktze., Stewart (1), 19, in large part.—CHARLES ISL.: 1000 ft., Stewart nos. 908 (K), 910 (NY). CHATHAM ISL.: Capt. Wood (K), as *Nephrodium molle*. INDEFATIGABLE ISL.: Rorud; Academy Bay, 850 ft., plants 4–5 ft. high, Svenson no. 133. JAMES ISL.: Darwin (as *N. molle*); James Bay, 2000 ft., Stewart no. 913 (K). Distributed throughout tropical America.

*Dryopteris pleiosora* (Hook.f.) n. comb. *Polypodium pleiosorum*<sup>9</sup> Hook.f. Trans. Linn. Soc. 20: 166 (1847) (as *pleiosoros*); Rob. (1), 113; Stewart (1), 25. *Nephrodium villosum* sensu Rob. (1), 110; non Presl. *Dryopteris villosa* sensu Stewart (1), 20; non Ktze. *Dryopteris tricholepis* sensu Stewart (1), 19 (partim); non (Bak.) C. Chr.—JAMES ISL.: Darwin (TYPE in herb. Cambridge Univ.). CHATHAM ISL.: Wreck Bay, common in moist places at 2000 ft., Stewart no. 914 (Cal, NY) (as *D. tricholepis*). GALAPAGOS IDS.: Capt. Wood (as *Polypodium Berteroanum*).

Darwin's specimen, which I examined at Cambridge, is the same as Capt. Wood's at Kew, the latter being slightly more hairy on the lower surface. Stewart's specimen at the California Academy of Sciences represents an entire frond with scattered and comparatively few sori; that at New York is very small and immature, but fortunately has the entire base which shows the typical *Ctenitis* scales exceptionally well. Throughout the rachis these scales appear to be homogeneous, a deep glossy brown,

<sup>9</sup> P. PLEIOSOROS, Hook. fil.; fronde ovatâ bipinnatâ, pinnis linearibus elongatis acuminatis; pinnulis lineari-oblongis approximatis apicibus rotundatis inferioribus grossè crenato-dentatis suprâ pilis sparsis hirtis subtùs molliter pubescentibus, soris 10–14, rachibus costisque pubescentibus paleaceisque.

Hab. James Island, Charles Darwin, Esq.

Rachis paleacea pilisque brevibus albidis obsita, paleis elongatis brunneis. Pinnae 6 unc. longae, ad medium lineares deinde ad acumen gradatim attenuatae, 1 unc. latae. Pinnulae sub-50,  $\frac{1}{2}$ – $\frac{2}{3}$  unc. longae,  $\frac{1}{4}$  latae, sessiles, membranaceae v. subcoriaceae, supernè confluentes, suprâ pubescentes, subtùs pilosae, pilis sparsis elongatis, marginibus supernè crenatae. Sori plurimi, medio venulae inter costam marginemque siti.



with well-developed marginal teeth. Short reddish articulate hairs occur abundantly on the lower surfaces of the frond, being replaced on the upper surfaces of the pinna-axis and the costules (especially on the nerves) by appressed subulate whitened hairs (of 4-6 cells, and averaging 0.2 mm. long), which make the surface somewhat glistening (at least in the Stewart specimens) and give a ciliate appearance to the margins of the segments. In addition, short two to three-celled hairs with a bulbiform apex (i.e. glandular) are found in mature segments (lacking in specimens at NY). The segments toward the middle of the frond are conspicuously crenate-dentate.

Capt. Wood's specimen, cited with doubt by Hooker (Sp. Fil. 4: 270 (1862)) under *Polypodium Berteroanum*, was distinguished as follows: "submembranaceous, segments elongated, lobes shorter, lowest inferior often forming an axillary lobe between two segments, probably distinct." Hooker's judgment seems to have been correct; the Galapagos plant is quite different from *Dryopteris inaequalifolia* (Colla) C. Chr. Vidensk. Skr. ser. 8, 6<sup>1</sup>: 73 (1920), [*Polypodium Berteroanum* Hook., not Sprengel] which is confined to Juan Fernandez, and has tripinnate fronds and prominent reddish scars on the stipe, left by the fallen scales. *D. tricholepis* (Bak.) C. Chr. is illustrated by Christensen (Vidensk. Selsk. Skr. ser. 7, 10<sup>2</sup>: 107, fig. 10d (1913)), and is obviously quite different from *D. pleiosora*, being an indusiate Guatemalan species with generally glabrous lower surfaces.

*D. POITEANA* (Bory) Urban, Symb. Ant. 4: 20 (1903); C. Chr. Vidensk. Selsk. Skr. ser. 7, 10<sup>2</sup>: 265 (1913). *Dryopteris reticulata* sensu Stewart (1), 19; not (L.) Urban.—INDEFATIGABLE ISL.: Academy Bay, occasional in damp woods, 800 ft., *Svenson* no. 107; Academy Bay, above 550 ft., *Stewart* no. 900 (Cal). According to Christensen (l.c.), *D. Poiteana* is a wide-ranging species found in most of the West Indian Islands and from Guatemala to Peru.

\**D. RUDIS* (Kze.) C. Chr. Ind. 289 (1905); Stewart (1), 19. *Polypodium rude* Kze. Linnaea 13: 133 (1839); Hook. Sp. Fil. 4: 243 (1862). Known only from the citation by Hooker (l.c.) "Galapagos, Wood?," and I could not locate the specimen at Kew.

*D. TETRAGONA* (Sw.) Urban, Symb. Ant. 4: 20 (1903). *D. pseudotetragona* Urban; Stewart (1), 19.—INDEFATIGABLE ISL.: the moist zone, December, 1926, *Rorud* no. 255; Academy Bay, in underbrush in damp places along trail, 700 ft., *Svenson* no. 117; Academy Bay, common in dense shade above 550 ft., *Stewart* no. 884 (Cal).

Christensen (l.c.) notes that the specimens collected by Miss Rorud are probably to be referred to a distinct form. The cutting of the pinnae

in no. 117 is very shallow, in this respect closely resembling the illustration of *D. Rolandii* C. Chr. Vid. Selsk. Skr. ser. 7, 10<sup>2</sup>: 258, fig. 45 (1913). The sporangia are not spinescent as in *D. Rolandii*.

#### ELAPHOGLOSSUM Schott

*E. PETIOLATUM* (Sw.) Urban, Symb. Ant. 4: 61 (1903); Stewart (1), 20. *Acrostichum muscosum* sensu Rob. (1) 104; non Sw. *A. viscosum* Sw.; Rob. (1) 105. *Elaphoglossum muscosum* (Sw.) Moore; Stewart (1), 20.—ALBEMARLE ISL.: Stewart no. 775 (Cal). (as *E. muscosum*). JAMES ISL.: Darwin (two sheets). The specimen noted as *Olfersia Langsdorffii* by Hook. f. (Trans. Linn. Soc. 20: 167 (1847)), has a linear-elliptic fertile frond with a long portion of the stipe. No scales appear on the rachis or elsewhere. The second Darwin specimen bears the annotation "very near *Acrostichum viscosum* var. *glabriusculum*." Both should be included under *E. petiolatum*; apparently the scaly-stiped *E. muscosum* (Sw.) Moore, is unknown from the Galapagos Islands.

#### HEMITELIA R. Br.

*H. aff. SUBCAESIA* Sodiro, Cr. Vasc. Quit. 522 (1893). *H. multiflora* sensu Stewart (1), 20; not (Sm.) R. Br.—ALBEMARLE ISL.: Stewart. CHATHAM ISL.: Stewart. JAMES ISL.: Stewart.

Stewart's collections (nos. 895–7) are quite different from true *H. multiflora* (illustrated by Maxon, Bull. Torrey Club 38: 545–550, pl. 35 (1911)). They have the general appearance of *Cyathea purpurea* of the West Indies. The large indusium is half-circular at the base, but cucullate and covering the entire sorus. The entire lower surface of the pinnules—at least in the younger stages—is covered by large appressed, flattened, ashy-gray scales, usually with hardened filamentous appendages. These are intermingled with smaller trichome-like scales and rigid short-jointed hairs.

#### HISTIOPTERIS Agardh

\**H. INCISA* (Thunb.) J. Sm. Hist. Fil. 295 (1875); Stewart (1), 21. *Pteris incisa* Thunb. Prod. Fl. Cap. 171 (1800); Rob. (1), 114.—The only specimen which I have seen is the collection by Capt. Wood (Kew), cited by Hooker, Sp. Fil. 2: 230 (1858). It consists of typical material with soft rounded pinnae, not yet in the fruiting stage. Stewart's misidentified collections (Cal) are *Pteridium arachnoideum* (no. 997) and *Pteris biaurita* (nos. 998, 999, 1000).

#### HYMENOPHYLLUM Sm.

*H. CILIATUM* Sw. in Schrad. Journ. 1800<sup>2</sup>: 100 (1801). *H. hirsutum* sensu Stewart (1), 21; not (L.) Sw.—CHATHAM ISL.: Wreck Bay, Stewart no. 898 (US).

## HYPOLEPIS Bernh.

*H. REPENS* (L.) Presl, Tent. Pterid. 162 (1836); Rob. (1), 109; Stewart (1), 21. *Lonchitis repens* L. Sp. Pl. 1078 (1753).—INDEFATIGABLE ISL.: Academy Bay, common in clearings, 800 ft., *Svenson* no. 109; south slope of mountain, 1625 ft., *Svenson* no. 131; 4-6 ft. high, forming much of the fern vegetation at 2000 ft., *Svenson* no. 147. GALAPAGOS IDS.: *Capt. Wood* (Kew), a poor specimen, cited by Hooker, Sp. Fil. 2: 64 (1858).

## NEPHROLEPIS Schott

*N. BISERRATA* (Sw.) Schott, Gen. Fil. ad t.3 (1834); Stewart (1), 21. *Nephrolepis acuta* Presl, Tent. Pterid. 79 (1836); Rob. (1), 110.—ABINGDON ISL.: 1650 ft. *Stewart*. ALBEMARLE ISL.: Villamil, near the shore, *Stewart* no. 921 (G). BINDLOE ISL.: common in the interior, *Stewart* no. 918 (G); *Snodgrass & Heller* no. 779 (G). WENMAN ISL.: in lava covers and on cliffs, *Stewart* no. 919.

*N. PECTINATA* (Willd.) Schott, Gen. Fil. ad t.3 (1834); Rob. (1), 110; Stewart (1), 22. *Nephrodium pectinatum* Presl; Hook.f. Trans. Linn. Soc. 20: 170 (1847).—ABINGDON ISL.: 1950 ft., *Stewart*. ALBEMARLE ISL.: Villamil, 1350 ft., *Stewart*. CHATHAM ISL.: Wreck Bay, 1800 ft., 2100 ft., *Stewart* no. 926 (G); southwest end, *Baur* no. 357 (G). DUNCAN ISL.: 1300 ft., *Stewart*. INDEFATIGABLE ISL.: Academy Bay, above 500 ft., *Stewart*; Academy Bay, an abundant epiphyte at 1100-1600 ft., *Svenson* no. 127; forming fern banks on the ground at 2000 ft., *Svenson* no. 222. JAMES ISL.: James Bay, lava crevices at 2150-2850 ft., *Stewart* no. 923 (G); *Darwin* (represented by two sheets), (as *Nephrodium pectinatum*).

## NOTHOLAENA R. Br.

*Notholaena galapagensis* Weatherby & Svenson, sp. nov. (Pl. 9, fig. 2). Rhizoma obliquum, breve repens, (2-4 cm. longum, 3 mm. diametro) paleis rigidis, reticulatis castaneis vel mature brunnescenti-fuscis lanceolatis vel lanceolato-ovatis (4-5 mm. longis, 1.3 mm. latis) haud denticulatis acuminatis concoloribus margine pallidior angustissimo saepe fere obsoleto excepto vestitum; folia subcoriacea, supra glabra, infra pulvere ceracea, subsulphurea obtecta; petiolus 4-12 cm. longus, brunneosubnitidus, ad basim paleis nonnullis divaricatis, semi-deciduis, brunnescenti-fuscis concoloribus reticulatis, attenuatis (3-3.5 mm. longis, 1 mm. latis) obsitus; lamina 5-11 cm. longa, 3-5 cm. lata ovato-oblonga bipinnatifida, deorsum in segmento primario tripinnatisecta; segmenta primaria opposita vel subopposita, infima 3 cm. distantia (3-4 cm. longa), breviter petiolata, anguste deltoideo-ovata, superiora sessilia oblonga, apice attenuata obtusa, pinnatipartita; laciniae vel segmenta secundaria coadunata oblonga obtusa, latere inferiore segmentorum infimorum non

auctis, omnia margine levissime crenulata; nervi immersi; sori nigricantes oligocarpi, frequenter monocarpi, sporangio maturo magno ( $330\mu$  diametro), massae ceraceae immersi, lineam intramarginalem efformantes, basi lobulis non scariosis cincti. *N. candidae* affinis, a qua inter aliis, squamis concoloribus segmentis infimis aequilateralibus stipite brunneo differt. *N. candida* (M. & G.) Hook. var. *lutea* (Cav.) Hook. Sp. Fil. 5: 111 (1864) as to plant, not as to name-bringing synonym. *Pteris lutea* sensu Hook.f. Trans. Linn. Soc. 20: 168 (1847), not Cav. Descr. 267 (1802). *N. sulphurea* sensu Rob., Proc. Am. Acad. 38: 111 (1902); Stewart, Proc. Cal. Acad. Sci. ser. 4, 1: 22 (1911); not J. Sm. in Seem. Bot. Voy. Herald 233 (1854), based on *Pteris sulphurea* Cav. Descr. 269 (1802).—ALBEMARLE ISL.: *Snodgrass & Heller; Stewart*. INDEFATIGABLE ISL.: Academy Bay, dry lava cliffs of escarpment at 100 ft., *Svenson* no. 79. JAMES ISL.: *Scouler* (Kew); *Stewart*. NARBOROUGH ISL.: *Stewart*. GALAPAGOS IDS.: *Cuming* no. 110 (Kew). As the TYPE, *Snodgrass & Heller* no. 23 (Gray Herbarium) from Iguana Cove, Albemarle Island is designated.

Historically Hooker's (1847) identification of Scouler's and Cuming's plants as *Pteris lutea* rested only on Sprengel's brief description (Syst. 4: 74 (1827)), in turn based on Cavanilles' description of a Mexican plant. Later Hooker (1864) treated the Galapagos plants as *Notholaena candida* without ascribing them to any definite variety, although the var. *lutea* in Hooker's somewhat confused account was made to include collections from Peru by Mathews and by Gillies. By Hooker & Baker (Syn. Fil. 373 (1868)), *N. candida* was further merged into the synonymy of *N. sulphurea* J. Sm., quite evidently the source of Dr. Robinson's employment of the latter name, which applies to a tripartite Mexican species.

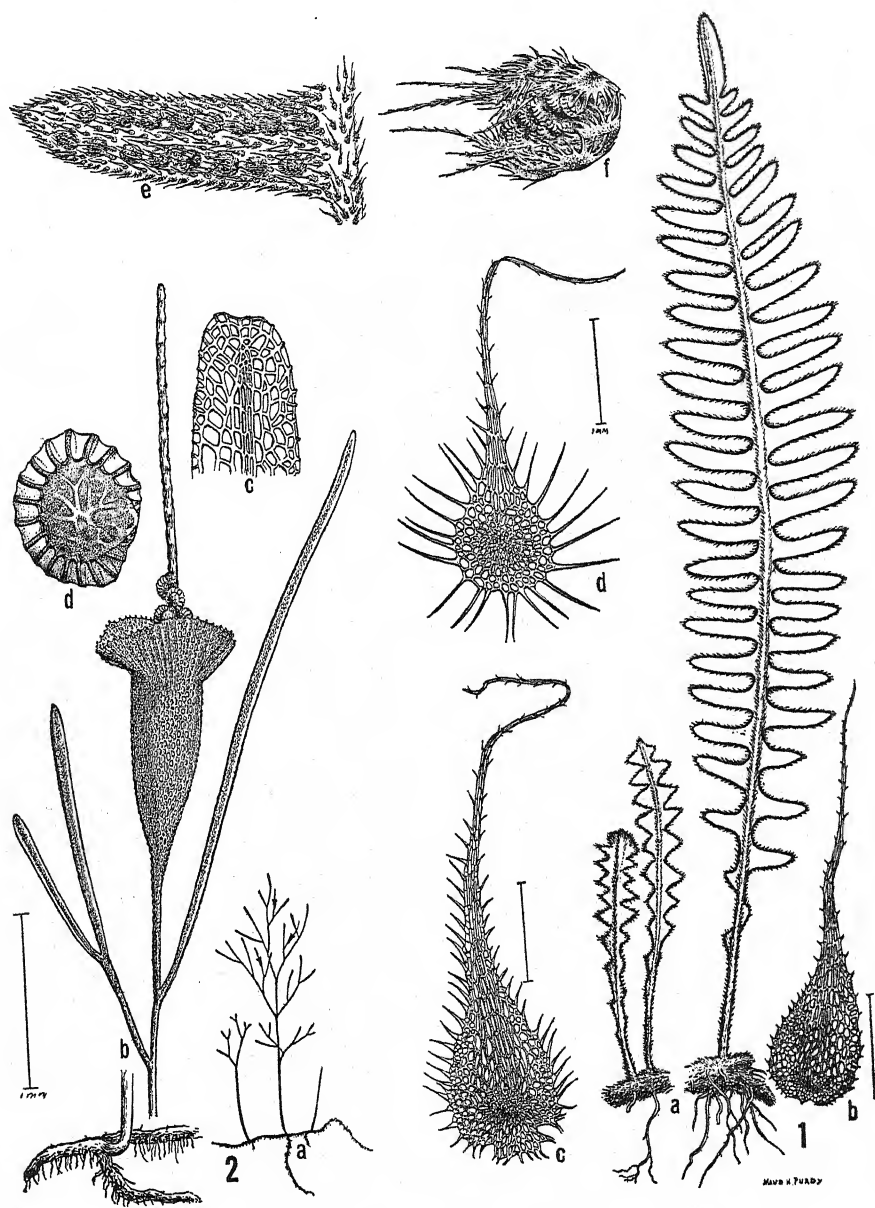
In reviewing the identity of *Pteris aurantiaca* and *P. lutea*, Christensen (Arkiv. f. Bot. 9<sup>o</sup>: 42 (1900) and Dansk Bot. Arkiv. 60, no. 3: 22 (1937)) finds that both are the same species i.e. *Cheilanthes lutea* (Cav.) Moore.

The yellow cera of the Galapagos plant consists of small stalked crateriform extrusions which are often linked up in the mature frond into a cobwebby mass. The sori are partially (sometimes wholly) covered by the revolute margin of the young frond; the mature sori are borne just within the revolute margin, only one sporangium in each sorus usually maturing. The sessile hemispheric sporangia average  $330\mu$  in width; the smooth dusky olivaceous spores are about the size of the spores of *Pellaea atropurpurea*.

#### Explanation of Plate 8

Fig. 1. POLYPODIUM LEPIDOPTERIS (no. 231): a, habit  $\times \frac{1}{2}$ . b, scale from rhizome. c, scale from stipe. d, scale from lower surface of pinna. e, lower surface of pinna ( $\times 2$ ). f, sorus, with adjacent scales.

Fig. 2. TRICHOMANES COCOS (no. 349): a, habit  $\times \frac{1}{2}$ . b, details of rhizome and tip of frond. c, apex of segment. d, sporangium.



SVENSON: PTERIDOPHYTA



The margin of the frond is unmodified, the cerate to somewhat glandular edge being without scales or hyaline tissue. Veins show only in the basal lobule of each segment, and as the midrib of the segment. The entire situation is much the same as in *E. J. Palmer* no. 13608 (*Notholaena candida*) except for a tendency in the latter toward transformation of the frond margin, thinner frond with obvious venation, and cerous trichomes (of different color than in *N. galapagensis*) on the upper surface of the frond as well as on the lower surface. *N. candida* also differs in having more approximate pinnae with linear-lanceolate divisions. The Galapagos plant is obviously not the same species; the difference is clear in illustrations by Martens & Galeotti and by Eaton.

Of the six species included by Mettenius (1859) in the group with fronds cerate on the lower surface, only *Cheilanthes affinis*, *C. candida*, and *C. monosticha* have lanceolate fronds. *C. monosticha* Mett. (based on *Ceropteris monosticha* Fée, Mém. 7: 44, t. 22, fig. 2 (1857) came from Mexico and was known to Mettenius only from Fée's description and plate. By Mettenius it was considered as scarcely distinct from *C. candida* except in the presence of a yellow instead of a white cera.

Hooker & Baker (l.c.) included several of Mettenius' species within *Notholaena sulphurea* J. Sm., with the following notation (p. 374): "We include here four species of Mettenius. His *C. Borsigiana*, Reichb., has the pinnae very close, and the lower pair much larger than the others, within the powder bright-yellow. From this *C. cretacea* seems to differ only by its white powder, and there are various intermediate stages. In *C. candida* and *monosticha* the pinnae are not so close and less unequal, the powder being white in the first and yellowish in the latter."

The type of *C. Borsigiana*, the only one of the group based on South American material (Peru), has been recently examined by Mr. Weatherby and found to be no more than a form of *Notholaena sulphurea*.

#### PITYROGRAMMA Link

P. CALOMELANOS (L.) Link, Handb. Gew. 3: 20 (1833); Maxon, Contr.

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#### Explanation of Plate 9

Fig. 1. POLYPODIUM aff. STEIROLEPIS (no. 93): a, habit  $\times \frac{1}{2}$ . b, scale from rhizome with (c) detail of lower portion. d, scale from stipe. e, sporangium.

Fig. 2. NOTHOLAENA GALAPAGENSIS (no. 79): a, habit  $\times \frac{1}{2}$ . b, scale from rhizome. c, scale from stipe. d, sterile pinnule, showing venation. e, fertile pinnule, showing margin. f, sporangium. g, cera (much enlarged).

Fig. 3. DIPLAZIUM aff. SUBOBTUSUM (no. 132): a, portion of frond,  $\times \frac{1}{2}$ . b, detail of lower part of a pinnule.





SVENSON: PTERIDOPHYTA

U. S. Nat. Herb. 17: 173 (1913). *Ceropteris tartarea* (Cav.) Link; Stewart (1), 16. *Gymnogramma tartarea* Desv. Berl. Mag. 5: 305 (1811); Rob. (1), 109.—ALBEMARLE ISL.: *Snodgrass & Heller*; *Stewart*. BINDLOE ISL.: *Stewart*. CHARLES ISL.: *Stewart*. CHATHAM ISL.: *Chiercha*; *Stewart*; *Baur*. DUNCAN ISL.: *Stewart*. INDEFATIGABLE ISL.: Academy Bay, locally in moist places among boulders, 1000–1100 ft., *Svenson* no. 218. JAMES ISL.: *Stewart*.

*P. PRESLIANA* Domin, var. *AURATA* Dom. Publ. Fac. Sci. Univ. Charles 88<sup>6</sup>: 19, t.1 (1929). *Gymnogramme tartarea* var. *aurata* Moore, Gard. Chron. 493 (1870).—BINDLOE ISL.: *Snodgrass & Heller* no. 778 (G), a juvenile specimen with flabellate fronds which are yellow-powdered on the under surface.

#### POLYPODIUM L.

*P. ANGUSTIFOLIUM* Sw. Prod. 130 (1788); Rob. (1), 111; Stewart (1), 23. *Marginaria ensifolia* Presl; Hook.f. Trans. Linn. Soc. 20: 167 (1847).—JAMES ISL.: *Darwin*; James Bay, 2100 ft., *Stewart* no. 935. Darwin's specimen at Cambridge is very doubtfully this species, and most probably *P. lanceolatum*.

*P. AUREUM* L. Sp. Pl. 1087 (1753); Rob. (1), 111; Stewart (1), 23. *Pleopeltis aurea* Hook.f. Trans. Linn. Soc. 20: 167 (1847).—ALBEMARLE ISL.: *Stewart*. DUNCAN ISL.: *Stewart*. JAMES ISL.: *Stewart*. GALAPAGOS IDS.: *Darwin*; *Capt. Wood*. The monstrous specimen collected by Darwin, which Hooker (l.c.) mentions, is clearly this species. I was unable to find *Capt. Wood's* specimen at Kew.

*P. CRASSIFOLIUM* L. Sp. Pl. 1083 (1753); Rob. (1), 112. Stewart (1), 23.—ALBEMARLE ISL.: Tagus Cove, *Stewart* no. 941 (perhaps *P. Phyllitidis*). GALAPAGOS IDS.: *Capt. Wood* (two sheets at Kew).

*P. LANCEOLATUM* L. Sp. Pl. 1082 (1753); Rob. (1), 112; Stewart (1), 23. *Pleopeltis macrocarpa* Kaul.f.; Hook.f., Trans. Linn. Soc. 20: 167 (1847). *Pleopeltis lepidota* Willd.; Hook.f. (l.c.).—ALBEMARLE ISL.: *Snodgrass & Heller*; *Stewart*. CHARLES ISL.: *Darwin*; *Andersson*; *Stewart*. DUNCAN ISL.: *Stewart*. INDEFATIGABLE ISL.: *Stewart*; Academy Bay, epiphyte, 400 ft., *Svenson* no. 56; 2000 ft., *Svenson* no. 213. JAMES ISL.: *Darwin*. Darwin's plant from James Island has wide fronds (3.3 cm.) identical with no. 213; his collection from Charles Island has fronds only 1 cm. wide.

*P. LEPIDOPTERIS* (Langsd. & Fisch.) Kze. Linnaea 13: 132 (1836), sensu lat.; Hook. Sp. Fil. 4: 212 (1862); Rob. (1), 112; Stewart (1), 23. ALBEMARLE ISL.: *Stewart*. DUNCAN ISL.: *Stewart*. INDEFATIGABLE ISL.: *Stewart*; Academy Bay, abundant epiphyte at 500 ft., *Svenson* no. 231

(Pl. 8, fig. 1). JAMES ISL.: *Stewart*. GALAPAGOS IDS.: *Capt. Wood* (2 sheets, the glistening, almost micaceous texture of the under surface, and the isolated deep brown scales of the rachis being especially noticeable). Stewart's nos. 452, 954, 955, and 956 are this species.

\**P. LORICEUM* L. Sp. Pl. 1086 (1753); Rob. (1), 112; Stewart (1), 24. Moore, Ind. Fil. 392 (1862).—GALAPAGOS IDS.: *Capt. Wood*. This collection at Kew (apparently the basis of Moore's citation) is identical with specimens collected by Seemann at the Bay of Cupica in 1848. Only a portion of the blade is present. This exceeds 40 cm. in length and 14 cm. across, with the acute pinnae up to 1.5 cm. wide, and the sori in several (often 4) rows.

*P. PECTINATUM* L. Sp. Pl. 1085 (1753); Rob. (1), 113; Stewart (1), 24. *P. paradiseae* Langsd. & Fisch. Ic. Fil. 11, t. 11 (1810–1818); Hook.f. Trans. Linn. Soc. 20: 165 (1847).—ABINGDON ISL.: *Stewart*. ALBEMARLE ISL.: *Snodgrass & Heller*; *Stewart*. CHARLES ISL.: *Andersson*; *Stewart*. CHATHAM ISL.: *Chiercha*; *Baur*; *Stewart*. INDEFATIGABLE ISL.: *Stewart*; Academy Bay, common on ground in underbrush 350–600 ft., *Svenson* no. 74. JAMES ISL.: *Darwin*; *Stewart*.

\**P. PERCUSSUM* Cav. Descr. 243 (1802); Hook. Fil. Exot. t. 59 & Sp. Fil. 5: 56 (1864); Rob. (1), 113; Stewart (1), 24.—GALAPAGOS IDS.: *Capt. Wood* (Kew). The frond is 3 cm. in diameter with prominent sori.

*P. PHYLLITIDIS* L. Sp. Pl. 1083 (1753); Rob. (1), 113; Stewart (1), 24. *Campyloneuron Phyllitidis* Presl; Hook.f. Trans. Linn. Soc. 20: 167 (1847).—INDEFATIGABLE ISL.: Academy Bay, 550 ft., *Stewart* no. 940 (Cal) (2 sheets, as *P. crassifolium*) (no. 941 not seen); Academy Bay, in shaded undergrowth near entrance to Plantation Fortuna, 700 ft., *Svenson* no. 114, and not uncommon to 1000 ft. JAMES ISL.: *Darwin*; above 1500 ft., *Stewart* no. 969. Also probably represented by "large sword ferns" (*Stewart* l.c.) on Abingdon Island.

*P. POLYPODIOIDES* (L.) Watt, Canad. Nat. II. 13: 158 (1867). *Polypodium incanum* Sw. Prod. 131 (1788); Hook.f. Sp. Fil. 4: 209 (1862); Rob. (1), 112 (only as to *Capt. Wood*'s collection).—ALBEMARLE ISL.: Villamil, common on the trunks of trees at 600 ft., *Stewart* no. 944. INDEFATIGABLE ISL.: Academy Bay, on the trunks and branches of trees above 425 ft., *Stewart* no. 942; southeast side, common on tree trunks at 625 ft., *Stewart* no. 943; *Rorud* no. 259. CHATHAM ISL.: *Capt. Wood*, a small specimen 6–7 cm. high, scales short and somewhat rufous.

*P. aff. STEIROLEPIS* C. Chr. Amer. Fern Journ. 7: 33 (1917). *P. thysanolepis* sensu Stewart (1), 26; not A. Br. ex Klotzsch.—ALBEMARLE ISL.: Villamil, abundant at 600 ft., on trees at 1300 ft., *Stewart* nos. 989 (Cal), 990 (Cal). INDEFATIGABLE ISL.: Academy Bay, epiphyte at 2000

ft., *Svenson* no. 93 (Pl. 9, fig. 1). JAMES ISL.: occasional on trunks of trees, 2750 ft., *Stewart* no. 991 (Cal).

Dr. Maxon has very kindly furnished the following comments on the specimens of my collection (no. 93):

The venation . . . is anomalous, being imperfectly goniophleboid, with an occasional indication of phleboid venation. Plants having the general aspect of no. 93 have commonly been referred to *P. leucosticton* Kunze, but mistakenly so, inasmuch as that species has winged stipes and free venation. Your plant is obviously related to *P. steirolepis* C. Chr., but that very critical species, as shown by several recent specimens, has definitely phleboid venation.

Another species that must be taken into account in this connection is *P. Fraseri* Mett., described from Ecuador. I have not seen the type of this or any authentic material; but I have removed from our cover of *P. leucosticton* a good many specimens from Colombia, Peru, and Ecuador which I now refer here tentatively, assuming that Mettenius's description was drawn from an under-sized specimen. In the character of the rhizome scales and in all real diagnostic features these plants agree with the description of *P. Fraseri*, and I think I am correct in referring them to that species, which in its rhizome scales (but not in several other characters) shows a very definite affinity to *P. leucosticton*. Your no. 93 can not be referred here nearly so well as to *P. steirolepis*, and my best judgment would be that you refer it, for the present, tentatively to *P. steirolepis*. It bears a very close general appearance to plants of that species and differs mainly in its less complicated venation. Possibly no. 93 represents a new species, but more probably it can be connected with typical *P. steirolepis* by plants showing intermediate stages of venation, when sufficient new material has been collected.

*P. TRIDENS* Kze. Farnkr. 1: t. 13, fig. 1 (1840); Hook. Sp. Fil. 4: 210 (1862). *P. squamatum* sensu Rob. (1), 113; Stewart (1), 25; not *L. Marginaria incana* Hook.f. Trans. Linn. Soc. 20: 166 (1847); Rob. (1), 113 (in part).—ABINGDON ISL.: *Snodgrass & Heller; Stewart*. ALBEMARLE ISL.: *Snodgrass & Heller; Stewart*. BINDLOE ISL.: *Snodgrass & Heller; Stewart*. CHARLES ISL.: *Darwin; Andersson; Capt. Markham (Kew); Lee; Baur; Stewart*. CHATHAM ISL.: *Capt. Wood; Snodgrass & Heller; Baur; Stewart*. DUNCAN ISL.: *Baur; Snodgrass & Heller; Stewart*. INDEFATIGABLE ISL.: *Stewart; Rorud*; terrestrial in thickets, half hidden by bushes, 500 ft., *Svenson* no. 73 (occasional at 250 ft., common at 450–600 ft.). JAMES ISL.: *Stewart*. JERVIS ISL.: *Stewart*. NARBOROUGH ISL.: *Stewart*. GALAPAGOS IDS.: *Cuming* no. 112.

*Marginaria incana*, from the Galapagos Islands, was known by Hooker as "var. frondibus plerumque pinnatis, pinnis inferioribus 2–3 furcatis." Darwin's specimens are *P. tridens*, as are also, without serious question, those of Macrae (specimens not seen). The collection by Capt. Markham has one pinna with five segments; otherwise it is like Cuming's type collection.

## POLYSTICHUM Roth

*P. aff. PYCNOLEPIS* Moore, Ind. 92 (1858). *P. aculeatum* sensu Stewart (1), 26; not (L.) Schott. ALBEMARLE ISL.: Villamil, 3150 ft., Stewart no. 802 (Cal).

*P. ADIANTIFORME* (Forst.) J. Sm. Hist. Fil. 220 (1875); Stewart (1), 26. *Aspidium coriaceum* Sw. in Schrad. Journ. Bot. 1800<sup>2</sup>: 40 (1801); Rob. (1), 106; *Polystichum coriaceum* Presl; Hook.f. Trans. Linn. Soc. 20: 171 (1847).—ALBEMARLE ISL.: Villamil, 3150 ft., Stewart no. 803 (Cal.) JAMES ISL.: Darwin. Darwin's two specimens agree well with other South American collections.

## PTERIDIUM Gled.

*P. ARACHNOIDEUM* (Kaulf.) Maxon, Journ. Wash. Acad. Sci. 14: 89 (1924). *P. aquilina* var. *esculenta* Hook.f. Fl. N. Zeal. 2: 25 (1855) and Hook. Sp. Fil. 2: 198 (1858); Rob. (1), 114; Stewart (1), 26.—ABINGDON ISL.: forms extensive brakes on the south side of the island above 1600 ft., Stewart no. 992; occasional around 1950 ft., Stewart no. 997 (Cal.) (as *Histiopteris incisa*). ALBEMARLE ISL.: Snodgrass & Heller; Stewart. CHATHAM ISL.: Baur; Stewart. INDEFATIGABLE ISL.: Academy Bay, forming thickets at 2000 ft., Svenson no. 212. GALAPAGOS IDS.: Capt. Wood, the collection closely resembling no. 212.

## PTERIS L.

\**P. PROPINQUA* var. *CUMINGIANA* Ag. Sp. Gen. Pterid. 65. (1839); Hook. Sp. Fil. 2: 223 (1858); Rob. (1), 115; Stewart (1), 26.—CHATHAM ISL.: Capt. Wood. The specimen at Kew, labeled "Chatham I." closely resembles Spruce no. 5708 from Guayaquil. In addition to the citation from the Galapagos Islands, var. *Cumingiana* is also mentioned by Hooker (l.c.) from Mexico to Venezuela and from the West Indies, and he further notes: "Of this *Pt. propinqua* I may observe, it will be difficult to distinguish it from some states of *Pt. aculeata*, Sw.; and the var. *Cumingiana* with its more rigid fronds, shorter more falcate, and often more mucronate segments, is, I fear, identical with *P. apicalis* of Liebmann." Capt. Wood's specimen apparently is the same as a fragment of the type collection at the U. S. National Herbarium.

*P. QUADRIAURITA* Retz. Obs. 6: 38 (1791). *Histiopteris incisa* sensu Stewart (1), 21; not (Thbg.) J. Sm.—ALBEMARLE ISL.: Stewart nos. 998 & 1000 (Cal) (as *H. incisa*).—INDEFATIGABLE ISL.: Academy Bay, occasional in shaded underbrush, 800 ft., Svenson no. 100. JAMES ISL.: James Bay, Stewart no. 999 (Cal) (as *H. incisa*). By Christensen (Index Filicum 593 (1906)), this species is included under *P. baurita* L.



## TECTARIA Cav.

*T. MARTINICENSIS* (Spr.) Copel. Phil. Journ. Sci. **2c**: 410 (1907). *Aspidium martinicense* Spr. Anleit. **3**: 133 (1804); Stewart (1), 13. *Nephrodium macrophyllum* Bak. Syn. Fil. 300 (1874); Rob. (1), 110.—ALBEMARLE ISL.: Stewart no. 902 (Cal). CHATHAM ISL.: Capt. Wood. JAMES ISL.: Stewart no. 903. Captain Wood's specimens at Kew are the same as Stewart's no. 903.

## TRACHYPTERIS André

*T. PINNATA* (Hook.f.) C. Chr. Ind. 634 (1906); Stewart (1), 27. *Hemionitis pinnata* Hook.f. Trans. Linn. Soc. **20**: 167 (1847). *Acrostichum aureo-nitens* Hook.f. Ic. Pl. **10**: t. 933 (1854); Rob. (1) 104.—ABINGDON ISL.: Stewart. ALBEMARLE ISL.: Snodgrass & Heller; Stewart. CHARLES ISL.: Darwin; Andersson; Lee; Baur; Stewart. CHATHAM ISL.: Capt. Wood; Stewart. INDEFATIGABLE ISL.: Stewart; Rorud; Academy Bay, abundant on exposed rocks, 100–300 ft. and on lava ledges in damp shaded woods, 400 ft., Svenson no. 226. JAMES ISL.: Stewart. NARBOROUGH ISL.: Snodgrass & Heller. GALAPAGOS IDS.: Capt. Wood; Capt. Markham.

This is perhaps the most spectacular fern of the Galapagos Islands. It can maintain itself on bare lava ledges, though fruiting specimens, in my experience, are confined to comparatively damp habitats. In addition, the species is known from the mainland, being represented by the following examples which I have examined; ECUADOR: Andibus merid. circa 3800 m., *E. André* no. 4699 (Kew). PERU: Colpapampa, 9000 ft., Bues no. 1339 (US); Toronton, 2000–2800 m., Herrera no. 1334 (US); Santa Ana, 900 m., Cook & Gilbert no. 1480 (US) & no. 1563 (US). BOLIVIA: Asilla, 3500 ft., R. S. Williams no. 1177 (NY); Espia, head of Bopi River, 3500 ft., Rusby no. 305 (B, NY).

The Brazilian plant, *T. Gilliana* (Baker) n. comb. (*Acrostichum Gillianum* Baker, Journ. Bot. 310 (1882)) from Arasenhay, Minas Geraes (Glaziou no. 1334) and "Catingawald bei Tambury," Bahia, Ule no. 7070 (Kew), does not apparently represent the same species as the Bolivian-Ecuadorian material, since in addition to the narrowly-trifid fertile pinnae the scales of the rachis are decidedly opaque as contrasted with the translucent scales of the plant from western South America. Furthermore, the fronds of Glaziou's collection are narrower, and hairy above as well as below. I can find no restriction of sporangia to the veins in dissecting the Galapagos specimens; the sporangia are borne over the entire frond surface. The genus would therefore seem to be close to *Elaphoglossum* (cf. however, Christensen, Dansk. Bot. Arkiv. **7**: 110 (1932)).



## TRICHOMANES L.

*T. KRAUSII* Hook. & Grev. Ic. Fil. 2: t.149 (1831). *Hymenophyllum Polynthos* sensu Stewart (1), 21; not Sw. *Trichomanes pusillum* sensu Stewart (1), 27.; not Sw.—DUNCAN ISL.: in dense tufts on the southeast side of rocks at 1300 ft., Stewart no. 899 (Cal) (as *H. polyanthos*). INDEFATIGABLE ISL.: Academy Bay, on dripping rocks, south slope of mountain, 1500 ft., Svenson no. 220. JAMES ISL.: James Bay, common on moist tufa walls at 2050 ft., Stewart no. 1013 (reported as no. 1012) (Cal) (as *T. pusillum*).

## SALVINIACEAE

## AZOLLA Lam.

*A. FILICULOIDES* Lam. Encyc. 1: 343 (1783). *A. caroliniana* sensu Rob. (1), 115; Stewart (1), 27; not Willd.—CHARLES ISL.: Andersson; Stewart no. 3441 (Cal). CHATHAM ISL.: Stewart no. 3442 (Cal). INDEFATIGABLE ISL.: abundant on the surface of pools west of Academy Bay, Svenson no. 86.

Although I have not seen Andersson's collection (reported as *A. caroliniana*) I have little hesitation in placing it under *A. filiculoides*, coming as it did from the same place as Stewart's collection.

## EQUISETACEAE

## EQUISETUM L.

*E. BOGOTENSE* HBK. Nov. Gen. & Sp. 1: 42 (1815); Stewart (1), 28.—ALBEMARLE ISL.: Stewart.

## LYCOPODIACEAE

## LYCOPODIUM L.

*L. CERNUUM* L. Sp. Pl. 1103 (1753).—INDEFATIGABLE ISL.: Rorud.

*L. CLAVATUM* L. Sp. Pl. 1101 (1753); Rob. (1), 115; Stewart (1), 28.—CHATHAM ISL.: Baur; Stewart. INDEFATIGABLE ISL.: Rorud; Academy Bay, abundant at 2000 ft., Svenson no. 207. JAMES ISL.: Stewart.

*L. COMPLANATUM* L. Sp. Pl. 1104 (1753); Stewart (1), 28.—ALBEMARLE ISL.: Stewart. INDEFATIGABLE ISL.: Rorud.

*L. DICHOTOMUM* Jacq. Enum. Vindob. 314 (1762); Rob. (1), 115; Stewart (1), 28.—ALBEMARLE ISL.: Stewart. INDEFATIGABLE ISL.: Stewart; Academy Bay, epiphyte, 400 ft. alt., Svenson no. 400.

*L. REFLEXUM* Lam. Encyc. 4: 653 (1789); Stewart (1), 28.—ALBEMARLE ISL.: Stewart.

*L. TAXIFOLIUM* Sw. Prod. 138 (1788).—CHARLES ISL.: Stewart. INDEFATIGABLE ISL.: Rorud; Academy Bay, epiphyte on *Xanthoxylon* trees at 1100–2000 ft., Svenson no. 208. JAMES ISL.: Stewart.

## PSILOTACEAE

## PSILOTUM Sw.

*P. NUDUM* (L.) Griseb. Abh. Ges. Wiss. Goettingen 7: 278 (1857). *P. triquetrum* Sw. in Schrad. Journ. Bot. 1800<sup>2</sup>: 109 (1801); Riley, Kew Bull. 1925: 231 (1925).—JAMES ISL.: Riley.

## COCOS ISLAND

(Only the pteridophytes collected by the Astor Expedition are included in this list.)

## FILICES

## ASPLENIUM L.

*A. MACRAEI* Hook. & Grev. Ic. Fil. t.217 (1831).—Wafer Bay, abundant on cliff walls at 700 ft., *Svenson* no. 339.

This material is exactly like the type from Hawaii collected by Macrae (Kew) and the same as the collection at Kew of *A. dubium* (*Brackenridge* no. 55, consisting of rather poor specimens) from the Fiji Islands (?). The specimens previously collected on Cocos Island under the name *A. cristatum* (*Stewart* no. 228) and as *A. rhizophyllum* (*Snodgrass & Heller* no. 954) are *A. Macraei*.

## DENNSTAEDTIA Bernh.

*D. GLOBULIFERA* (Poir.) Hieron, in Engler, Bot. Jahr. 34: 455 (1904).—Wafer Bay, abundant from near sea level to above 1000 ft., *Svenson* no. 343.

## DANAEA J. E. Smith

*D. NODOSA* (L.) Sm. Mém. Ac. Turin 5: 420 t.9, fig. 11 (1793).—Wafer Bay, abundant in alluvial soil along brook, *Svenson* no. 328 (Pl. 10). I am of the opinion that the "small palms" in Stewart's illustration, pl. 33 (op. cit.) are this species.

## DICRANOPTERIS Bernh.

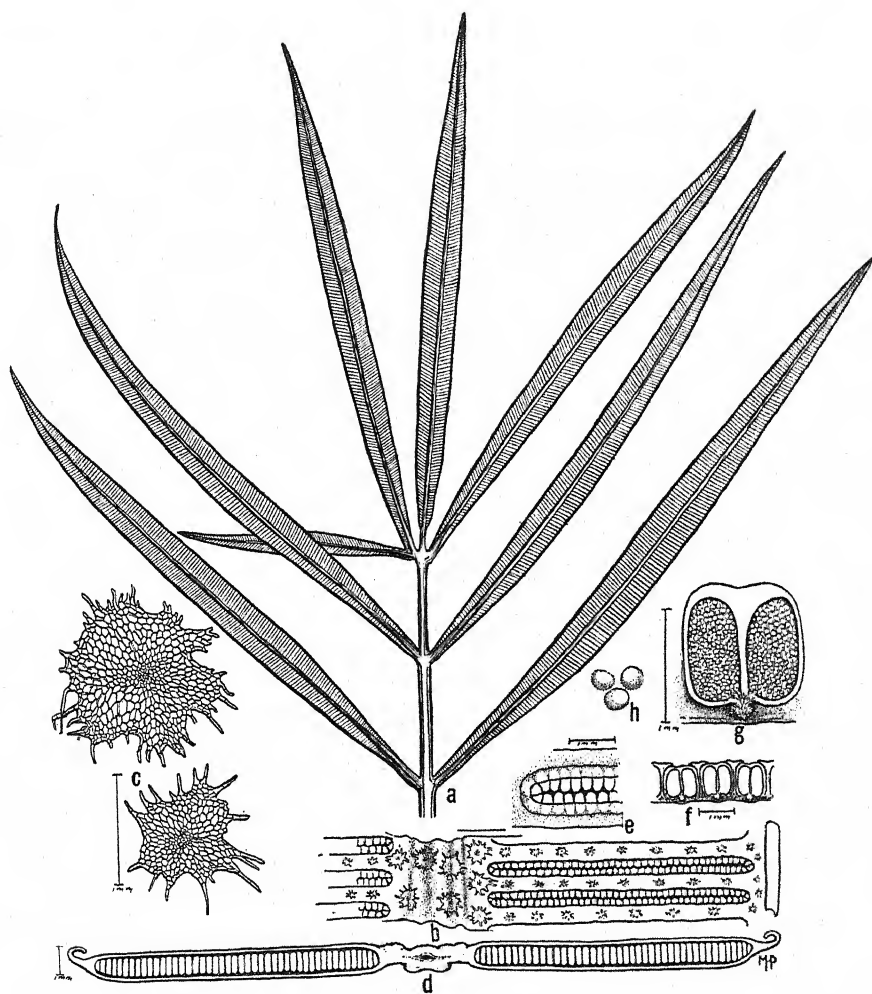
*D. PECTINATA* (Willd.) Underw. Bull. Torrey Club 34: 260 (1907). *Mertensia pectinata* Willd. Sv. Vet. Akad. Handl. ser. 2, 25: 168 (1804).—Wafer Bay, covering banks of stream at 150 ft., *Svenson* no. 332.

## ELAPHOGLOSSUM Schott

*E. APODUM* (Klf.) Schott, Gen. Fil. ad t.14 (1834). *Acrostichum*

## Explanation of Plate 10

Pl. 10. *DANAEA NODOSA* (no. 328): a, tip of frond  $\times \frac{1}{2}$ . b, portion of fertile pinna (lower surface) with enlarged scales (c) and as seen in cross section (d). e-h, details of sporangia and spores.



*apodum* Kaulf. Enum. 59 (1824).—Wafer Bay, epiphyte at 1000 ft., *Svenson* no. 403.

E. CRINITUM (L.) Christ, Mon. 112, fig. 53 (1899). *Acrostichum crinitum* L. Sp. Pl. 1068 (1753).—Wafer Bay, epiphyte on trunks of tree ferns, 1000 ft., *Svenson* no. 402.

HYMENOPHYLLUM J. E. Smith

H. POLYANTHOS Sw. in Schrad. Journ. 1800<sup>2</sup>: 102 (1801).—Wafer Bay, on mossy tree trunks at 1000 ft., *Svenson* no. 345.

HYPOLEPIS Bernh.

H. aff. VISCOSA (Karst.) Mett. Ann. Sc. Nat. V. 2: 238 (1864) (nomen); Karst. Fl. Col. 2: 89, t. 145, 146 (1869).—Wafer Bay, along brook up to 800 ft., *Svenson* no. 341.

LINDSAEA Dryand

L. MONTANA Fée, Mém. Foug, 11: 17, t. 6, fig. 2 (1866).—Chatham Bay, along brook near sea level, *Svenson* no. 433.

NEPHROLEPIS Schott

N. BISERRATA (Sw.) Schott, Gen. Fil. ad pl. 3 (1834). *Aspidium biserratum* Sw. in Schrad. Journ. Bot. 1800<sup>2</sup>: 32 (1801).—Wafer Bay, banks of the stream at 150 ft., *Svenson* no. 350.

OLEANDRA Cav.

O. ARTICULATA (Sw.) Presl, Tent. Pter. 78 (1836). *Aspidium articulatum* Sw. in Schrad. Journ. Bot. 1800<sup>2</sup>: 30 (1801).—Chatham Bay: an abundant epiphyte, *Svenson* no. 312.

POLYBOTRYA Humb. & Bonpl.

POLYBOTRYA CERVINA (L.) Klf. Enum. 55 (1824). *Osmunda cervina* L. Sp. Pl. 1065 (1753).—Wafer Bay, on ground along brook, 200–1000 ft., *Svenson* no. 342.

POLYBOTRYA SP. Wafer Bay, in rock crevices and on the ground 800 ft., *Svenson* no. 340 (young plants).

POLYPODIUM L.

P. ASTROLEPIS Liebm. Dansk. Vid. Selsk. Skrift. V. 1: 185 (1849); Weatherby, Contrib. Gray Herb. no. 65: 6 (1922).—Wafer Bay, a common epiphyte along brook, *Svenson* no. 321.

P. LATUM (Moore) Sodiro, Crypt. Vasc. Quit. 371 (1893). *Camploneurum latum* Moore, Ind. Fil. 225 (1861).—Chatham Bay, abundant on hillsides and along streams, *Svenson* no. 311.

## SACCOLOMA Kaulf.

*S. ELEGANS* Kaulf. Berl. Jahrb. Pharm. 1820: 51 (1820).—Wafer Bay, rather common on ground in shady places, 300 ft., *Svenson* no. 336.

## TRICHOMANES L.

*T. Cocos* Christ, Bull. Boiss. II. 4: 943 (1904).—Wafer Bay, abundant on trunks of tree ferns at app. 1000 ft., *Svenson* no. 349 (Pl. 8, fig. 2).

This endemic species, closely related to *T. capillaceum* L., is described as having the pinnae more sprawling so that the frond becomes flabellate at its periphery. The segments are said to be thicker and somewhat dilated at the ends, and the receptacles less open; the color of the plant, in general, is darker.

*T. ELEGANS* Rich. Act. Soc. Hist. Nat. Paris 1: 114 (1792).—Chatham Bay, dark moist places beneath ledges; fronds bluish-green. Common to 1000 ft., and probably above, *Svenson* no. 313, alt., 50 ft.

*T. GALEOTII* Fourn. Bull. Soc. Fr. 15. 144, 147 (1868).—Wafer Bay, epiphyte with translucent fronds, at 800 ft., *Svenson* no. 407.

*T. HOOKERI* Presl., Abh. Boehm. Ges. Wiss. v. 3. 108 (1843).—Wafer Bay, on a decayed stump at 800 ft. but not otherwise noted. *Svenson* no. 344.

*T. RADICANS* Sw. in Schrad. Jour. 1800:<sup>2</sup> 97 (1801).—Chatham Bay, abundantly climbing on damp rocks and tree trunks, but only one clump seen in fruiting stage, 800 ft., *Svenson* no. 328.

## VITTARIA J. E. Smith

*V. LINEATA* (L.) Sm., Mém. Acad. Turin 5: 413, pl. 9, fig. 5 (1793). Wafer Bay, epiphyte near sea level, *Svenson* no. 330.

## LYCOPODIACEAE

## LYCOPODIUM L.

*L. PITTIERI* Christ, Bull. Soc. Bot. Genève, ser. 2, 1: 236 (1909). Wafer Bay, a fairly common epiphyte, the branches hanging vertically, *Svenson* no. 324. (det. W. R. Maxon).

## SELAGINELLACEAE

## SELAGINELLA Beauv.

*S. HORIZONTALIS* (Presl) Spring, Mon. Lycop. pt. 2, 264 (1848). Wafer Bay, beneath trees near beach, *Svenson* no. 320. (det. A. H. G. Alston).

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## The American Species of *Dryopteris*, subgenus *Meniscium*<sup>1</sup>

WILLIAM R. MAXON AND C. V. MORTON

(WITH PLATES 11-14)

With the exception of the subgenus *Meniscium* the American ferns of the genus *Dryopteris* were treated monographically by Christensen in 1907, 1913, and 1920. His work upon this difficult group, which had been distinguished (even among the ferns) for its widely overlapping and confused specific concepts and its exceedingly complicated synonymy, was based upon an enormous amount of material brought together from the larger European herbaria and the U. S. National Museum, and is of outstanding importance and permanent value. *Meniscium* was omitted because the series of specimens at hand was not sufficiently comprehensive.

That a revision of *Meniscium* is still sorely needed was brought home to us forcefully in a recent effort to identify an interesting Ecuador specimen collected by Mrs. Ynes Mexía, and the present paper has resulted from an effort to reduce the existing confusion. For the loan of much recent and valuable material we are indebted to the following institutions: Botanisches Museum, Berlin; Botanisk Museum, Copenhagen; Field Museum of Natural History; Gray Herbarium of Harvard University; Royal Botanic Gardens, Kew; New York Botanical Garden.

The first knowledge of a fern of this group comes from Plumier,<sup>2</sup> who in 1693 gave a description and plate of a plant called *Filix latifolia, non ramosa nigris tuberculis pulverulenta*. The same plate (with a slightly amplified description) was reproduced by him in 1705<sup>3</sup> under the name *Lingua cervina nigris tuberculis pulverulenta*. A little later Petiver<sup>4</sup> depicted the same species under the name *Phyllitis ramosa striis undulatis*. From the nomenclatural point of view, the first species to be proposed was that described by Linnaeus<sup>5</sup> as *Polypodium reticulatum*, his description reading as follows: "*P. frond. pinnatis oblongis integris, anastomosantibus rectangulis, punctis rectangulis approximatis. Plum. t. 9.*"

Later, Jacquin<sup>6</sup> described from Martinique a species which he called *Asplenium sorbifolium*, citing the same Plumier plate that formed the basis

<sup>1</sup> Published by permission of the Secretary of the Smithsonian Institution.

<sup>2</sup> Description des Plantes de l'Amérique 6. pl. 9. 1693.

<sup>3</sup> Traité des Fougères de l'Amérique 92. pl. 110. 1705.

<sup>4</sup> Pteridographia Americana pl. 7, fig. 1. 1712.

<sup>5</sup> Syst. Nat. ed. 10, 2: 1325. 1759.

<sup>6</sup> Coll. Bot. 2: 106. pl. 3, fig. 2. 1788.

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of *Polypodium reticulatum* L. Jacquin's own description and figure leave no doubt that his species is identical with that of Linnaeus, a fact duly recognized by Schreber<sup>7</sup> in proposing the genus *Meniscium*. His description is as follows: "*Meniscium* Schreb. *Asplenium* Jacq. Coll. 2 t. 3. f. 2 *Polypodium reticulatum* L. *Capsulae congestae in lunulas, venulis frondis interjectis*." The type species of *Meniscium* is therefore *Polypodium reticulatum* L.

The genus *Meniscium* was promptly accepted and its validity was not questioned for nearly 70 years. It was still recognized by Mettenius in 1856,<sup>8</sup> but in 1859<sup>9</sup> he reversed his earlier opinion and united it with *Phegopteris*, a procedure entirely contrary to our modern ideas of nomenclature, inasmuch as *Phegopteris* dates, as a genus, only from 1852. In any case Mettenius' systematic views were not shared by Hooker and Baker, who continued to recognize the genus *Meniscium*, a usage which occasionally continued as late as 1910. A union of this group of species with *Nephrodium* was proposed by Keyserling<sup>10</sup> and accepted by Diels.<sup>11</sup> Transfers to *Dryopteris* were first made by Urban<sup>12</sup> and were continued by Christensen in the Index Filicum.

Within the genus *Dryopteris*, the subgenus *Meniscium* is most closely related to *Goniopteris* section *Microdictyon*, which includes *D. Poiteana* (Bory) Urban, *D. Liebmanni* Maxon & Morton,<sup>13</sup> and *D. Ghiesbreghtii* (Linden) C. Chr. These species all have essentially meniscioid venation, but are distinguished from true *Meniscium* by their paired sori, which have the receptacle more or less elevated and rotund, never elongate. Such sori are not found in *Meniscium* except sporadically and, presumably, as an atavistic condition. Moreover, all species of *Goniopteris* have stellate hairs, at least on the rhizome scales, but these have not been found in *Meniscium*, except in *D. Desvauxii* forma *glandulosa*, in which a very few large multiradiate hairs are on close examination occasionally to be seen near the base of the costules.

An affinity with the subgenus *Stigmatopteris* is also evident through the aberrant species *D. Christii* C. Chr., which was described by Baker as *Meniscium opacum*. Here the venation is meniscioid and the receptacle

<sup>7</sup> Linnaeus, Gen. Plant. ed. 8, 2: 757. 1791.

<sup>8</sup> Filices Lechlerianae, part 1. 1856.

<sup>9</sup> Op. cit. part 2. 1859.

<sup>10</sup> Polypod. Cyath. Herb. Bung. 1873.

<sup>11</sup> Die Natürlichen Pflanzenfam. 1: pt. 4. 1899.

<sup>12</sup> Symb. Antill. 4: 1903.

<sup>13</sup> *Dryopteris Liebmanni* Maxon & Morton, nom. nov.

*Polypodium meniscioides* Liebm. Dansk. Vid. Selsk. Skrift. V. 1: 211. 1849.

*Dryopteris meniscioides* C. Chr. Ind. Fil. 277. 1905, not Kuntze (1891).

elongate, but the nearer relationship with *Stigmatopteris* is evident in the glabrous lamina, which is regularly pinnatifid at apex, rather than imparipinnate, and in the presence of scales along the costules. In *Meniscium* scales along the costae and costules are never found. Even along the rachis and stipe they are usually caducous.

The Old World species which have been referred to *Meniscium* are considerably different from any American species and are, as Christensen<sup>14</sup> suggested, probably not to be associated in the same subgenus with them.

The first comprehensive account of *Meniscium* was by Fée,<sup>15</sup> who listed 15 species, seven of which were new. He divided the species into two sections, one strictly Old World, characterized by having the sporangium-sac setose, the other, entirely American, with non-setose sporangium-sac. The American species were in turn divided into two groups, one characterized by hirsute sori, the other by glabrous sori. Fée's keen discernment of these critical differences was unjustly ignored by subsequent fern students. The hirsute character of the sori of certain species is usually obvious, even on casual inspection. A closer examination shows that the setiform hairs arise, not from the receptacle, but from the sporangium stalks near their apex. These we believe to afford an important character, separating the species into natural groups. The species proposed by Fée are mostly valid, although some of his names are antedated by those of other authors.

In determining the presence or absence of setae on the stalks of the sporangia a close scrutiny with the higher power of a dissecting microscope is often necessary, although in *Dryopteris Hostmanni*, *D. permollis*, and *D. Desvauxii* the setae are usually clearly visible with a hand lens or even with the naked eye. In counting the number of areoles and the number of lateral veins within a space of three centimeters we have selected the middle or lower portion of middle or lower pinnae of mature plants, inasmuch as the areoles are naturally fewer and the veins closer together near the apex of the pinnae, and of course the same condition is found in upper or juvenile pinnae.

The following account is far from satisfactory, owing partly to the lack of complete material suitable for comparison, the fronds as a rule being coarse and ill-suited to collecting in their entirety. In particular, a number of critical specimens from Bolivia have necessarily been left unplaced. Certain species also, like *D. Jurgensenii* and *D. Desvauxii*, are remarkably variable in size and general appearance. On the whole, however, the species are more readily recognizable than is indicated by the key. Their

<sup>14</sup> Monogr. Dryopteris 1: 268. 1913.

<sup>15</sup> Gen. Fil. 221-225. 1852.

number is almost certain to be increased, when additional material from Bolivia and several other regions becomes available for study.

## KEY TO SPECIES

**Fronds simple**

- Blades large (up to 60 cm. long and 12.5 cm. broad), acuminate, the midrib appressed-pubescent; stipes dull, puberulent, palaeaceous; areoles 30-40-seriate; sori linear, nearly straight  
15. *D. simplicifrons*
- Blades small (up to 12.5 cm. long and 4 cm. broad), caudate-acuminate, the midrib glabrous; stipes lustrous, glabrous, naked.....4. *D. minuscula*

**Fronds pinnate**

Pinnæ uncinat-serrate, at least toward apex.

Upper pinnæ often reduced; pinnæ gradually attenuate from a broad base, mostly stalked, the uppermost sessile; veins and usually the leaf tissue strongly pubescent.....5. *D. serrata*

Upper pinnæ not reduced; pinnæ very narrowly oblong, rather abruptly acuminate-caudate at apex, mostly sessile, several of the uppermost semiadnate to short-decurrent; veins and leaf tissue glabrous.....6. *D. consobrina*

Pinnæ undulate, crenulate, or usually subentire.

Stalk of sporangium without hairs.

Pinnæ 2-5-jugate.

Blades conform; pinnæ 4.5-7.5 cm. broad; lateral veins of fertile pinnæ 4-11 pairs per 3 cm.; areoles 13-20-seriate.

Pinnæ rounded, obtuse, or broadly cuneate at base, subsessile; lateral veins 8-11 pairs per 3 cm.; sporangia aggregate in single linear sori.....2. *D. Andreana*

Pinnæ cuneate, the lower ones strongly so, stalked (up to 2.5 cm.); lateral veins 4-6 pairs per 3 cm.; sporangia often arranged in paired sori.....1. *D. Ungulata*

Blades subdimorphic; pinnæ 2.5-4.5 cm. broad; lateral veins of fertile pinnæ 13-18 pairs per 3 cm.; areoles 7-10-seriate.....3. *D. arcana*

Pinnæ many-jugate.

Areoles of sterile pinnæ almost as long as broad, the secondary veins nearly straight.

Pinnæ linear, often falcate.

Pinnæ entirely glabrous, the lower ones subcordate, sessile.....10. *D. ensiformis*

Pinnæ hairy on veins, the lower ones cuneate at base, long-petiolate.....11. *D. Jurgensenii*

Areoles of sterile pinnæ much shorter than broad, the secondary veins curving and arcuate, subsigmoid.

Sterile pinnæ up to 22 cm. long and 3 cm. broad; lateral veins of fertile pinnæ 12-18 pairs per 3 cm. (except in *D. nesiotica*); areoles 4-12-seriate; fertile pinnæ contracted and much smaller than the sterile, except sometimes in *D. Salzmanni*.

Sterile pinnæ 1-2 (2.3) cm. broad, subequally cuneate at base, mostly stalked, the basal ones strongly so; areoles 4-8-seriate. Lateral veins of sterile pinnæ 11-18 pairs per 3 cm.; pinnæ long-attenuate.....12. *D. angustifolia*

Sterile pinnæ 1.7-3 cm. broad, obtuse or rounded at base, or oblique at upper side, sessile; areoles 8-12-seriate.

Pinnæ long-attenuate; lateral veins of fertile pinnæ 8 pairs per 3 cm.....13. *D. nesiotica*

Pinnæ acute or short-acuminate; lateral veins of fertile pinnæ 12-16 pairs per 3 cm.....7. *D. Salzmanni*

Sterile pinnæ often over 30 cm. long, 3.5-6.5 cm. broad, long-acuminate; lateral veins of fertile pinnæ 7-10 pairs per 3 cm.; areoles 13-22-seriate; fertile pinnæ usually conform with sterile.

Pinnæ broadest at middle.....8. *D. turrialbae*

Pinnæ broadest in lower third.....9. *D. reticulata*

Stalk of sporangium bearing near apex 1 or more sharply pointed setae (obvious as hairs among the sporangia) or (in *D. Desvauxii* f. *glandulosa*) these rarely with a blunt glandular apex.

Blades subdimorphic, the fertile pinnae suffused with sporangia; sterile pinnae much larger (mostly 5-7 cm. broad).

Pinnae few, subentire.....21. *D. chrysodioides*

Pinnae numerous, the fertile ones deeply crenate to irregularly repand-crenate; plants much larger.....21a. *D. chrysodioides* var. *goyazensis*

Blades not dimorphic, the fertile pinnae usually with discrete sori; sterile pinnae commonly less than 4 cm. broad (up to 6 cm. in *D. membranacea*).

Areoles 3-5-seriate; pinnae rounded-auriculate at base, slightly constricted above base.....14. *D. dispar*

Areoles 7-20-seriate; pinnae not auriculate, not constricted above base

Lower pinnae rounded at base, sessile or nearly so; areoles 11-20-seriate.

Pinnae caudate-acuminate, 4-6 cm. broad; sterile areoles commonly rounded; lateral veins of fertile pinnae 6 or 7 pairs per 3 cm.....16. *D. membranacea*

Pinnae acute or attenuate, 2.5-4 cm. broad; sterile areoles acute; lateral veins of fertile pinnae 13-15 pairs per 3 cm.....17. *D. Standleyi*

Lower pinnae cuneate at base, petiolulate; areoles 5-12-(rarely 15-) seriate.

Leaf surface almost invariably glabrous between the veins. Pinnae narrow (2 cm. broad or less); areoles 7-9-seriate.....18. *D. Hostmanni*

Leaf surface hairy, often densely and softly so, or the hairs replaced by capitate glands.

Pinnae large (usually over 20 cm. long and 3 cm. broad), the lowest with a petiolule at least 1 cm. long.

Leaf hairs conspicuous, setiform.....19. *D. Desvauxii*

Leaf hairs replaced by capitate glands.....19a. *D. Desvauxii* f. *glandulosa*

Pinnae smaller, the lowest with a petiolule not more than 5 mm. long. Leaf surface densely pilose.....20. *D. permollis*

1. DRYOPTERIS LINGULATA C. Chr. Dansk. Vid. Selsk. Skrift. VII. Naturv. Afd. 10<sup>2</sup>: 271. 1913.

In this species the arcuate venules are often sterile at the middle and thus have a pair of sori, instead of a single linear sorus. This condition is occasionally noted in other species also and can not be considered as of special significance, except perhaps as indicating that *D. lingulata* is one of the more primitive species of this alliance. The paired sori are always elongate, and never have a definite rotund receptacle as in *Goniopteris* or in some of the Old World species that have been referred to *Meniscium*.

We have examined the following specimens:

COSTA RICA: Valley of Río Hondo, near Madre de Diós, in forest, alt. 200 meters, *Pittier* 10349, type coll. (US). Hamburg Finca, on Río Reventazón below Cairo, Prov. Limón, alt. 55 meters, in wet forest, *Standley* & *Valerio* 48659 (US). Finca Hundrisser, *Brade* 306 (Y).

PANAMA: Foothills of Garagará, Sambu Basin, southern Darien, alt. 30-500 meters, *Pittier* 5596 (US).

COLOMBIA: Tutenendo, 20 km. north of Quibdó, Intendencia del Chocó,



alt. 80 meters, *Archer* 2130 (US). Landázuri region, Dept. Santander, alt. 300 meters, along streams, *Mrs. Geo. L. Green* 51 (US).

PERU: San Antonio, on Río Itaya, Dept. Loreto, alt. 110 meters, in dense forest, *Killip & Smith* 29378 (US.)

2. *DRYOPTERIS ANDREANA* (Sod.) C. Chr. Ind. Fil. 252. 1905.

*Meniscium Andreanum* Sod. Recens. 71. 1883; Crypt. Vasc. Quit. 392. 1893.  
*Phegopteris Andreana* Christ in Pitt. Prim. Fl. Costar. 3: 35. 1901, as to name.

*Dryopteris Andreana* var. *glabra* Hieron. Hedwigia 46: 352. 1907.

Founded on specimens collected along the Río Toachí, near Santo Domingo, Ecuador, and known to us only from that country.

Undoubtedly *D. Andreana* is most closely related to *D. lingulata* C. Chr., which is of very similar aspect but may be distinguished by the cuneate-based petiolulate lower pinnae, those of *D. Andreana* being rounded and sessile. We consider this an important character in *Meniscium*. The Costa Rican record for *D. Andreana*, published by Christ, was based on *Pittier* 10349, a collection which later served as the type of *D. lingulata*.

ECUADOR: In silv. apud Los Colorados, Oct. 1883, *Sodirol* (K, 3 sheets). In silv. reg. Angamarca, Nov. 1900, *Sodirol* 310 (Y, 3 sheets). In silv. trop. sec. fl. Pilatón, 1899, *Sodirol* (Y). In silv. trop. et subtrop., alt. 400–1800 m., *Sodirol* (US). Base of Mt. Chimborazo, alt. 900 m., July 1860, *Spruce* 5739 (K). Near Mindo, *Stübel* 767 (B, type of *D. Andreana* var. *glabra*). Nanegal, *Sodirol* 54/6 (K). Road from Quito to Manabí, *Sodirol* 54/8 (K).

3. *Dryopteris arcana* Maxon & Morton, sp. nov.

PLATE 11

Rhizoma breviter repens, vix 1 cm. diam. Folia usque ad 85 cm. longa, laxe suberecta, subbiformia, omnino glabra, stipitibus e basi fusca dilute olivaceis sulcatis, eis foliorum steriliū laminas subaequantibus, eis fertiliū quam laminis multo longioribus; lamina 1-pinnata; pinnae 2 vel 3-jugae et terminalis conformis major, infimae plerumque suboppositae, ceterae alternae et remotae. Laminae steriles ambitu orbiculari-ovatae, 18–30 cm. longae, 14–20 cm. latae, rachi tenui; pinnae obliquae, margine subintegrae, anguste oblongae, 10–18 cm. longae, 2.5–4.5 cm. latae, apice longe acuminatae, basi subanguste cuneatae, infimae petiolulatae (3–9 mm.); venae laterales ca. 50-jugae, spatio 3 cm. 10–13, sub angulo 60° egredientes, prominulae; venulae sub angulo 45° eductae, angulo recto vel subacuto conjunctae, subtus promin-

Explanation of Plate 11

Plate 11. *Dryopteris arcana* Maxon & Morton, sp. nov. The type specimen; Ecuador, *Mexia* 7174. About half natural size.





MAXON & MORTON: DRYOPTERIS

ulae; areolae 7-10-seriatae, venulis excurrentibus elongatis liberis; parenchyma chartacea. Laminae fertiles ovatae vel oblongae; pinnae porrectae, margine irregulariter repando-crenatae, plerumque lanceolatae, 7-12 cm. longae, 1.5-2.5 cm. latae, in apicem caudatum sensim attenuatae, basi anguste cuneatae, plerumque breviter petiolulatae (infimae usque ad 1 cm.); venae laterales spatio 3 cm. 13-18, subflexuosae; venulae sub angulo lato egredientes, arcuatum conjunctae; areolae 8-10-seriatae, breves, plerumque fertiles; sori oblongi, brunnei, discreti sed vetuste interdum subconfluentes.

Type in the U. S. National Herbarium, no. 1,691,406, collected on the trail from Tena to Napo, Province of Napo-Pastaza, Ecuador, at an altitude of 400 meters, on a steep wet bank in shade, April 5, 1935, by Mrs. Ynes Mexía (no. 7174). Two additional specimens of this number have furnished data for the description.

*Dryopteris arcana* is not closely related to the other pinnate species, but shows an undoubted affinity with *D. minuscula*, despite the simple fronds of the latter. The veins diverge at a much wider angle, however, and the pinnae are not abruptly caudate, as is the blade of *D. minuscula*.

4. DRYOPTERIS MINUSCULA Maxon, Kew Bull. Misc. Inf. 1932: 135. 1932.

This species, evidently rare, is known only from the type material at Kew, which was found by Lehmann (no. 4433) on moist earth banks and rock walls along the Río Dagua, coastal region of Buena Ventura, Colombia. It is by no means closely related to *D. simplicifrons*, the only other species with simple fronds, from which it differs in aspect, size, and gross morphology too widely for comparison, as well as in its non-appendiculate sporangia. Its relationship is doubtless with *D. arcana*, as mentioned.

5. DRYOPTERIS SERRATA (Cav.) C. Chr. Ind. Fil. 291. 1905.

*Meniscium serratum* Cav. Descr. Pl. 548. 1803.

*Meniscium dentatum* Presl, Del. Prag. 1: 162. 1822.

*Meniscium palustre* Raddi, Opusc. Sci. Bol. 3: 284. 1819; Pl. Bras. 1: 9. pl. 20. 1825.

*Meniscium rostratum* Fée, Gen. Fil. 224. pl. 18 B, fig. 3. 1852.

*Phegopteris palustris* Mett. Fil. Lechl. 2: 24. 1859.

*Phegopteris serrata* Mett. Ann. Sci. Nat. V. Bot. 2: 243. 1864.

*Nephrodium serratum* Keys. Pol. Cyath. Herb. Bung. 49. 1873.

*Dryopteris reticulata* var. *serrata* Farwell, Amer. Midl. Nat. 12: 292. 1931.

*Thelypteris serrata* Alston, Kew Bull. Misc. Inf. 1932: 309. 1932.

The present species, described originally from Habana, is exceedingly variable, but, though widely distributed, it gives no evidence of regional segregation. A distinctive character is found in the margins, which, at least near the apex of the pinnae, are uncinat-serrate. From *D. consobrina*,

the only other species with similar margins, *D. serrata* is distinguished by the key characters. Occasionally the margins are deeply jagged and erose-serrate. In certain other species of *Meniscium* the margins are often crenate or crenulate, especially in the fertile pinnae, but only in this species and *D. consobrina* are they ever truly serrate. Sometimes also, as in other species, minutely paleaceous buds are borne on the costae of the lower pinnae, at or just above their base. These occasionally develop into small plants. An extreme case is shown by a frond from Morro das Pedras, State of São Paulo, Brazil, *Brade* (Y), in which the young plants are 15 cm. high.

As to range: *D. serrata* occurs in Florida, but is uncommon in the West Indies, except in Trinidad; on the continent it ranges from Mexico to Paraguay and Argentina, being abundant in Brazil. Material of this species has mostly not been borrowed by us. The following list includes the numbered specimens examined, these mainly in the National Herbarium:

FLORIDA: Southern shore of Lake Okeechobee, *Harshberger* in 1912 (Y).

JAMAICA: *Wilson* 518; *Bot. Dept.* 332; *Sherring*.

CUBA: *Léon* 2404; *Hioram & Maurel* 4698.

PUERTO RICO: *Sintenis* 6378.

GUADELOUPE: *Duss* 1612.

TRINIDAD: *Fendler* 57 (9 sheets); *Britton, Hazen, & Freeman* 948; *Hart* 554; *Broadway* 2778; *Jenman*; *Kuntze*.

MEXICO: *Fisher* 35387; *Orcutt* 6628; *Purpus* 8602; *Ross* 1064; *C. L. Smith* 2111.

GUATEMALA: *Barber* 167; *Kellerman* 7360; *Lundell* 3297; *Maxon & Hay* 3056; *J. D. Smith* 2421.

HONDURAS: *Ames* 172; *Dyer* A 146; *Standley* 53701, 53784; *Thieme* (*J. D. Smith* 5660 and 5695); *Yuncker* 5049.

COSTA RICA: *Pittier* 10265; *J. D. Smith* 6934; *M. Valerio* 19, 891; *Werckle*.

PANAMA: *Bailey* 401, 476; *Dodge* 3453; *Kenoyer* 23; *Killip* 2819; *Maxon* 4782, 6723; *Seibert* 641; *Skutch* 2; *Stork* 105.

COLOMBIA: *H. H. Smith* 1055; *Killip & Smith* 14924; *Haught* 1596; *Holton* 30; *Pennell & Rusby* 51; *Schott*.

VENEZUELA: *Rusby & Squires* 378; *Pittier* 10879.

BRITISH GUIANA: *Gleason* 471, 786; *De La Cruz* 3449; *Graham* 379; *Jenman*.

FRENCH GUIANA: *Sagot* 720.

BRAZIL: *Burchell* 1529, 9882; *Dusén* 11469, 14733; *Haerchen* (*Rosen-*

stock 72); *Lützelburg* 12918; *Martius* 357; *Pickel* 2251; *Regnell* III. 1444 in part; *Schmalz* 57; *L. B. Smith* 2008; *Wacket* 96.

PARAGUAY: *Balansa* 2830; *Fiebrig* 999; *Hassler* 1539, 4835, 5476; *Jorgensen* 4607.

ARGENTINA: Orán, El Cedral, Prov. Salta, *Rodriguez* 1035. Alrededores de Posadas, Misiones, *Núñez* 234.

ECUADOR: Balao, *Eggers* 14396.

PERU: *Killip & Smith* 27036; *Klug* 431; *L. Williams* 4236.

BOLIVIA: *Bang* 554 in part; *Steinbach* 7500.

6. *Dryopteris consobrina* Maxon & Morton, sp. nov.

Rhizoma deest. Folia suberecta, usque ad 2.15 m. longa, stipitibus validis (maximis 115 cm. longis, basi 1 cm. diam.), e basi brunnea dilute brunnescentibus, crasse angulato-sulcatis, primum tenuiter et minute puberulis; lamina 1-pinnata, late oblonga, usque ad 1 m. longa et 70 cm. lata, rhachi stipiti simili; pinnae 9-11-jugae et terminalis conformis, subpatentes (maximae 25-30 cm. longae et 3.5-5 cm. latae), anguste lineari-oblongae, apice acuminate-caudatae, basi modice rotundatae vel interdum subabrupte et late cuneatae, subaequales, pleraeque sessiles, solum subapicales plurimae postice semiadnatae, omnes margine callosa argute dentato-serratae, serraturis imprimis pinnae apicem versus uncinatis, parenchyma glabra; venae laterales infra acuminem 60-65-jugae, plerumque 6-8 spatio 3 cm. (raro usque ad 13), sub angulo 70° egredientes, utrinque prominulae, leviter falcatae, subtus pilis obliquis brevibus perpaucis praeditae; areolae 12-22-seriatae, breves, steriles venulis inaequalibus obliquis formatae, fertiles venulis sub angulo latissimo eductis et arcuatim conjunctis formatae; sori anguste oblongi, propinqui sed vetuste etiam non confluentes; sporangia glabra.

Type in the U. S. National Herbarium, nos. 1,464,533 and 1,464,534 (a sterile frond) and no. 1,692,123 (basal portion of a fertile frond), collected in a wooded valley near La Merced, Dept. Junín, Peru, altitude about 700 meters, June 4, 1929, by E. P. Killip and A. C. Smith (no. 24087). Duplicate in herb. New York Botanical Garden. Other specimens examined:

PERU: Type locality, *Killip & Smith* 23514 (US, Y). Río Apurimac Valley, near Kimpitiriki, alt. 400 meters, edge of dense forest along beach, *Killip & Smith* 22945 (US, Y).

In its uncinately-serrate margins the present species resembles *D. serrata*, from which, highly variable though the latter is, it is readily distinguished as above indicated. The Apurimac Valley specimen (*Killip & Smith* 22945) clearly belongs to *D. consobrina*, but it is under-sized and its dimensions are not included in the description.

7. *Dryopteris Salzmanni* (Fée) Maxon & Morton, comb. nov.

*Meniscium Salzmanni* Fée, Gen. Fil. 223. 1853.

*Meniscium elongatum* Fée, Crypt. Vasc. Brés. 1: 83. pl. 25, fig. 1. 1869.

?*Meniscium sessilifolium* Pohl; Fée, op. cit. 84.

This species was described by Fée from Bahia material collected by Salzmann. It has very generally been disregarded, most specimens having been referred to *D. reticulata*, which in every way is a much larger plant. The pinnae of *D. Salzmanni* are more rigid and ascending and have fewer, more acute areoles. The relationship is probably somewhat closer to *D. serrata* than to *D. reticulata*.

Specimens examined are as follows:

BRAZIL: State of Bahia: Bahia, *Salzmann*, type coll. (B, C, Y); *Glocker* 189 (K). State of Rio de Janeiro: Without locality, *Glaziou* 1169, type coll. of *M. elongatum* (C); Serra dos Orgaos, near Pereira, *Lützelburg* 6024 (C, US); Corcovado, *Voy. Herald* 167 (K); Organ Mts., alt. 1000-1500 meters, *Rose & Russell* 20803 (US, Y); Mt. Itatiaya, alt. 800 meters, *L. B. Smith* 1648 (C, US). State of Minas Geraes: Viçosa, alt. 680 meters, *Mexia* 4683 (US), 4857a (US); Lagoa Santa, *Warming* 793 (C, 4 sheets). State of Maranhao: Victoria Alto Parnahyba, *Snethlage* 724 (F). State of São Paulo: Campinas, *Ulbricht* (*Rosenstock* 215) (US). Without locality, *Glaziou* 15744 (C).

COLOMBIA: Without locality, *Funck & Schlim* in 1862 (Y).

PERU: Pampayaco, alt. 1050 meters, *Macbride* 5046 (US). Zepelacio, near Moyobamba, alt. 1100-1200 meters, *Klug* 3354 in greater part (K, US, Y). Valley of Pillahuata, Province of Paucartambo, *Herrera* 1622 (US).

8. *DRYOPTERIS TURRIALBAE* Rosenst. Repert. Sp. Nov. Fedde 22: 10. 1925.

A Costa Rican form, described from specimens collected on the lower Atlantic slopes near Turrialba, altitude 650 meters, Aug. 1909, by Alfredo and Curt Brade (no. 357). It is by far the most weakly characterized of any of the species here recognized and may prove no more than a geographic variety of the West Indian *D. reticulata*, from which it differs mainly in the shape of the pinnae. The following collections have been studied:

COSTA RICA: Turrialba, alt. 650 meters. *A. & C. Brade* 357, type coll. (Y); Banks of Río Colorado, near Turrialba, alt. 600 meters, *Tonduz* 8287 (US). Tuis, Prov. Cartago, alt. 650 meters, *Tonduz* 11321 (K, US); same, distributed as *J. D. Smith* 7325 (K, US).



9. *DRYOPTERIS RETICULATA* (L.) Urban, Symb. Antill. 4: 22. 1903.

*Polypodium reticulatum* L. Syst. Nat. ed. 10, 2: 1325. 1759.

*Asplenium sorbifolium* Jacq. Coll. Bot. 2: 106. pl. 3, fig. 2. 1788.

*Meniscium sorbifolium* Dessrous. in Lam. Encyl. 4: 93. 1797.

*Meniscium Schreberi* Rich. Act. Soc. Hist. Nat. (Paris) 1: 114. 1792 (nomen nudum).

*Meniscium reticulatum* Sw. Journ. Bot. Schrad. 1801<sup>2</sup>: 274. 1803.

*Diplazium undulosum* Sw. Syn. Fil. 92, 284. 1806, in part (as to Plum. Trait. Foug. pl. 107).

*Meniscium acrostichoides* Desv. Mém. Soc. Linn. Paris 6: 223. 1827.

*Phegopteris reticulata* Mett. Fil. Lechl. 2: 24. 1859.

*Phegopteris sorbifolia* Mett. op. cit. 23.

*Nephrodium reticulatum* Keys. Pol. Cyath. Herb. Bung. 49. 1873.

*Nephrodium sorbifolium* Hieron. Bot. Jahrb. Engler 34: 449. 1904, as to name; not Presl (1825).

*Dryopteris reticulata* var. *sorbifolia* Suesseng. Rev. Südamer. Bot. 1: 82. 1934.

As previously stated, the sole basis of Linnaeus' description of *Polypodium reticulatum* is the Plumier illustration (plate 9, republished as plate 110). This was cited also under *Asplenium sorbifolium* by Jacquin, whose diagnosis leaves no doubt that he was redescribing the Linnaean species under another name. This identity was recognized by early authors; but later writers, beginning perhaps with Schott, wrongly associated the name *sorbifolium* with a South American species (*D. Hostmanni*) that is not very closely related to *D. reticulata* and is not known to occur in the West Indies. Still later the name came to be applied generally but very mistakenly to the species which we here call *D. permollis*.

Due allowance being made for age and varying habitat, *D. reticulata* is a very constant species. The following specimens, mainly in the National Herbarium, have been examined:

FLORIDA: Alapattah, on cypress knees, Eaton 779 (US, Y).

JAMAICA: Alexander; Clute 149; Fredholm 3209; Maxon 1004, 1710, 2282, 2371, 2552, 8948, 9358, 10323; Maxon & Killip 24, 502, 1542; Underwood 2986; Watt 162.

CUBA: Britton et al. 5142, 7537, 14742; Clément 1313; Eggers 5019; Hioram 1396, 6457; Linden 2116; Maxon 4208, 4254; Palmer & Riley 82, 917, 1026, 1048; Pollard et al. 48; Shafer 4366, 8568, 8955, 10651, 10688, 13689; Wright 782, 1084.

HISPANIOLA: Abbott 37, 74, 77, 610, 746, 1442, 2166; Eggers 2315; Ekman 3823, 11549; Fuertes 1682; Leonard 9188; Miller 1162; Nash & Taylor 1053; Valeur 336, 827.



PUERTO RICO: *Britton et al.* 8398; *Eggers* 724; *Fisher* 69 in part; *Goll* 682; *Heller* 1034; *Hioram* 87; *Shafer* 3232; *Sintenis* 132, 2338, 6584; *Stevenson* 6120; *Underwood & Griggs* 267, 530.

LEEWARD ISLANDS: St. Kitts, *Box* 263; *Britton & Cowell* 181. Guadeloupe, *Stehlé* 511, 654, 1096, 1876. Dominica, *Bailey* 763.

WINDWARD ISLANDS; Montserrat, *Miller* 1924; *Ryan* 169; *Shafer* 202, 736, 738; *Turner*. Martinique, *Duss* 1611; *Hahn* 29; *Iseri* in 1787; *Miller* in 1924; *Thiébaud* in 1876. St. Vincent, *Guilding*. Grenada, *Eggers* 6057; *Murray & Elliott* 11; *Sherring* 35. St. Lucia, *Box* 452, 491.

ISLAND OF MARGARITA (Venezuela); Juan Griego trail, alt. 450 meters, *Johnston* 166 (6 sheets). El Valle, *Miller & Johnston* 156 (3 sheets).

The altitudinal range is from sea-level to a maximum of 900 meters.

10. DRYOPTERIS ENSIFORMIS C. Chr. Dansk. Vid. Selsk. Skrift. VII. Naturv. Afd. 10<sup>2</sup>: 269. fig. 46. 1913.

Founded on a Costa Rican plant (*Tonduz* 12533), and now to be reported also from Peru and Venezuela. We regard this as an excellent species, although the points stressed by Christensen do not seem of special significance. These were: (1) The presence of an aerophore, (2) the cartilaginous margins, and (3) the long excurrent venules, which often are extended to the next cross-veins. The aerophore was not seen but was postulated from the presence of a dark spot upon the rachis at the base of the pinnae. This was considered to be the scar of a fallen aerophore. But these spots are to be observed in most if not all species of *Meniscium*, and although we have examined a great amount of material we have found no evidence of aerophores. On the contrary these dark spots themselves, which are verruculose, presumably function as ventilation areas. Cartilaginous margins are common to other large coarse species of *Meniscium*. As to venation, the fact that the excurrent venules are sometimes united to form a more or less continuous intermediate vein parallel to the true lateral veins is not a distinctive character, this condition being quite as common in *D. Jurgensenii*. In the type collection of *D. ensiformis* the sori are commonly though not always paired, but this is not true in other specimens of this species. As mentioned under *D. lingulata*, paired sori in this group may be regarded as an abnormal atavistic condition.

*Dryopteris ensiformis* is most closely related to *D. Jurgensenii*, from which it differs in having the pinnae sessile and subcordate at base (in decided contrast to the cuneate-based, long-stalked lower pinnae of the latter), and in its wholly glabrous blades, at least a few hairs being found along the costae and veins of *D. Jurgensenii*.

The following specimens have been examined:

COSTA RICA: Lisière des Paturâges à La Palma, alt. 1459 meters, *Tonduz* 12533, type coll. (C, US); *C. Brade* 104 (US). Without locality, *Werckle* (US).

PERU: Schunke Hacienda, above San Ramón, Dept. Junín, alt. 1400–1700 meters, in forest, *Killip & Smith* 24651 (US, Y).

VENEZUELA: Near Tovar, *Fendler* 232 in part (B).

11. *Dryopteris Jurgensenii* (Fée) Maxon & Morton, comb. nov.

*Meniscium falcatum* Liebm. Dansk. Vid. Selsk. Skrift. V. 1: 183. 1849.

*Meniscium Jurgensenii* Fée, Gen. Fil. 223. 1852 (as *M. Jungersenii*).

*Phegopteris falcata* Mett. Fil. Lechl. 2: 23. 1859.

*Dryopteris pachysora* Hieron. Hedwigia 46: 351. pl. 7, fig. 9. 1907.

*Dryopteris sorbifolia* var. *confertivenosa* Hieron. op. cit. 350.

*Dryopteris sorbifolia* var. *punctivenulosa* Hieron. loc. cit.

*Dryopteris falcata* C. Chr. Dansk. Vid. Selsk. Skrift. VII. Naturv. Afd. 10<sup>2</sup>: 270. 1913, not Kuntze (1891).

The present species, latterly recognized as valid, was first described as *Meniscium falcatum* Liebm., but unfortunately this epithet is invalid under *Dryopteris*. *Meniscium Jurgensenii* Fée, founded on *Jurgensen* 917 from Mexico, is obviously the same.

*Dryopteris Jurgensenii* is now found to be common, ranging from southern Mexico to Bolivia. In spite of very considerable extremes in size, the specimens here cited are relatively constant in venation. The venules are straight or nearly so and meet at a broad angle, and the false intermediate lateral veins sometimes formed by the intermittently joined excurrent venules imperfectly divide the areoles into trapeziform halves. This is markedly different from the condition seen in *D. reticulata*, *D. Salzmanni*, and most other species, in which the venules are obviously curved (subsigmoid), at least in the sterile pinnae.

The following specimens have been examined:

MEXICO: Near Lacoba, Distr. Chinantla, Puebla, alt. 600–750 meters, *Liebmann* 679, 680, 2756, type of *M. falcatum* (C, K, US).

BRITISH HONDURAS: Big Creek, near sea level, along river banks, *Schipp* 97 (C, F, K, US).

GUATEMALA: Near Finca Sepacuité, *Cook & Griggs* 667 (US). Livingston, *Deam* 453 (Y). Sierra del Mico, alt. 600 meters, *Kellerman* 7212 (F). Puerto Barrios, at sea level, *Standley* 25003 (US), 25017 (US). Cubilquitz, Alta Verapaz, alt. 350 meters, *Tuerckheim* (*J. D. Smith* 8039) (US).

NICARAGUA: Castillo El Viejo, along Río la Juana, *Shimek* (F). San Juan del Norte, *C. L. Smith* 2030 (US, Y).

COSTA RICA: Llanuras de San Carlos, alt. 200 meters, *Brade* 485 (Y).

Pejivalle, *Lankester* 819 (US). Buenos Aires, in forest, *Pittier* 4839 (US). El General, Prov. San José, alt. 950 meters, *Skutch* 2181 (US).

PANAMA: Chagres, *Fendler* 404 (K, US). Near Laguna de Chiriquí, *Hart* 16 (US). Hilly forest near Las Cascadas, Canal Zone, alt. 50-225 meters, *Maxon* 4895 (US). Along Río Culebra, above Santa Isabel, Prov. Colón, near sea level, *Pittier* 4153 (US). Near San Felix, eastern Chiriquí, *Pittier* 5209 (US).

COLOMBIA: Bay of Utria, *Seemann* (K). Monte la Tortuga, *García* 4600 (US). Puerto Berrio, Dept. Santander, alt. 100-700 meters, *Haught* 1842 (US). Chocó, *Schott* 24 & s. n. (F, US, Y); *Seemann* 972 (K). Between Honda and Bogotá, *Stübel* 392, type of *D. sorbifolia* var. *confertivenosa* (B). Near Muzo, Dept. Cundinamarca, *Stübel* 544, type of *D. sorbifolia* var. *punctivenulosa* (B). Without locality, *Lehmann* 5034 (K, US); *Mutis* 3299 (US).

PERU: East of Quimiri Bridge, near La Merced, Dept. Junín, alt. 800-1300 meters, in forest, *Killip & Smith* 23890 (US, Y). Pichis Trail, Yapas, Dept. Junín, alt. 1350-1600 meters, in forest, *Killip & Smith* 25570 (US, Y).

BOLIVIA: Hacienda Simaco, on road to Tipuani, alt. 1400 meters, *Buchtien* 5158 (C, US, Y). Apolo, alt. 150 meters, *R. S. Williams* 1254 (Y).

12. DRYOPTERIS ANGUSTIFOLIA (Willd.) Urban, Symb. Antill. 4: 21. 1903.

*Meniscium angustifolium* Willd. Sp. Pl. 5: 133. 1810.

*Phegopteris angustifolia* Mett. Fil. Lechl. 2: 22. 1859.

This species, here taken up in the usual sense, was founded on a Caracas specimen collected by Bredemeyer. It had been described and illustrated originally by Sloane<sup>16</sup> as "*Filix major in pinnas tantum divisa oblongas angustatas, non crenatas.*" Both specimens have been examined by the senior author, at Berlin and the British Museum (Natural History).

*Dryopteris angustifolia* is common in the Greater Antilles, ascending from sea level to about 700 meters, but is unknown from the Lesser Antilles. On the continent it ranges from Costa Rica to Paraguay, reaching an altitude of 1100 to 1400 meters in Colombia, but oddly enough is apparently wanting in Brazil. In all probability the continental range could be considerably amplified by examining material in other herbaria. Most of the following specimens are in the U. S. National Herbarium.

JAMAICA: *Clute* 270; *Crawford* 805; *Hart* 346; *Maxon* 799, 1824, 8851; *Maxon & Killip* 144.

CUBA: *Clément* 1785; *Hioram* 1479; *Maxon* 4319; *Wright* 781.

HISPANIOLA: *Abbott* 2017, 2579; *Ekman* 5638, 12298; *Leonard* 8730, 12296; *Miller* 1133; *Nash & Taylor* 1221; *Valeur* 319.

<sup>16</sup> Nat. Hist. Jamaica 1: 84. pl. 40. 1707.

PUERTO RICO: *Britton et al.* 3935, 8429, 8580; *Dale* 10; *Eggers* 1336; *Heller* 1398; *Hess* 339; *Hioram* 264; *Shafer* 3144; *Sintenis* 4547, 4657; *Wilson* 53, 348.

MEXICO: Lacoba, Chinantla, Puebla, *Liebmann*.

GUATEMALA: Near Mazatenango, *Bernoulli* 446.

COSTA RICA: La Fortuna, *Biolley* in 1906. Pasoagres, near Alajuela, *Lankester* 605.

PANAMA: Chagres, *Fendler* 397. Juan Diaz River, *Killip* 2559. Río Tapia, Prov. Panamá, *Standley* 28122. Obispo, Canal Zone, *Standley* 31692.

COLOMBIA: Santa Marta, *Mrs. Dora Bennett* 29; *Niemeyer* 36; *H. H. Smith* 1053. East of Zarzal, Dept. El Valle, *Pennell*, *Killip & Hazen* 8538, 8583. Without locality, *Mutis* 3284. Dibulla, Dept. Magdalena, *Seifriz* 279 in part.

PERU: Río Paucartambo Valley, near Perene Bridge, Dept. Junín, *Killip & Smith* 25260. Chazuta, Río Huallaga, Dept. San Martín, *Klug* 4035. San Buenaventura, *Cárdenas* 1899.

BOLIVIA: Mapiri, alt. 650 meters, *Tate* 413 (Y).

PARAGUAY: Sierra de Amambay, *Hassler* 10508 (K).

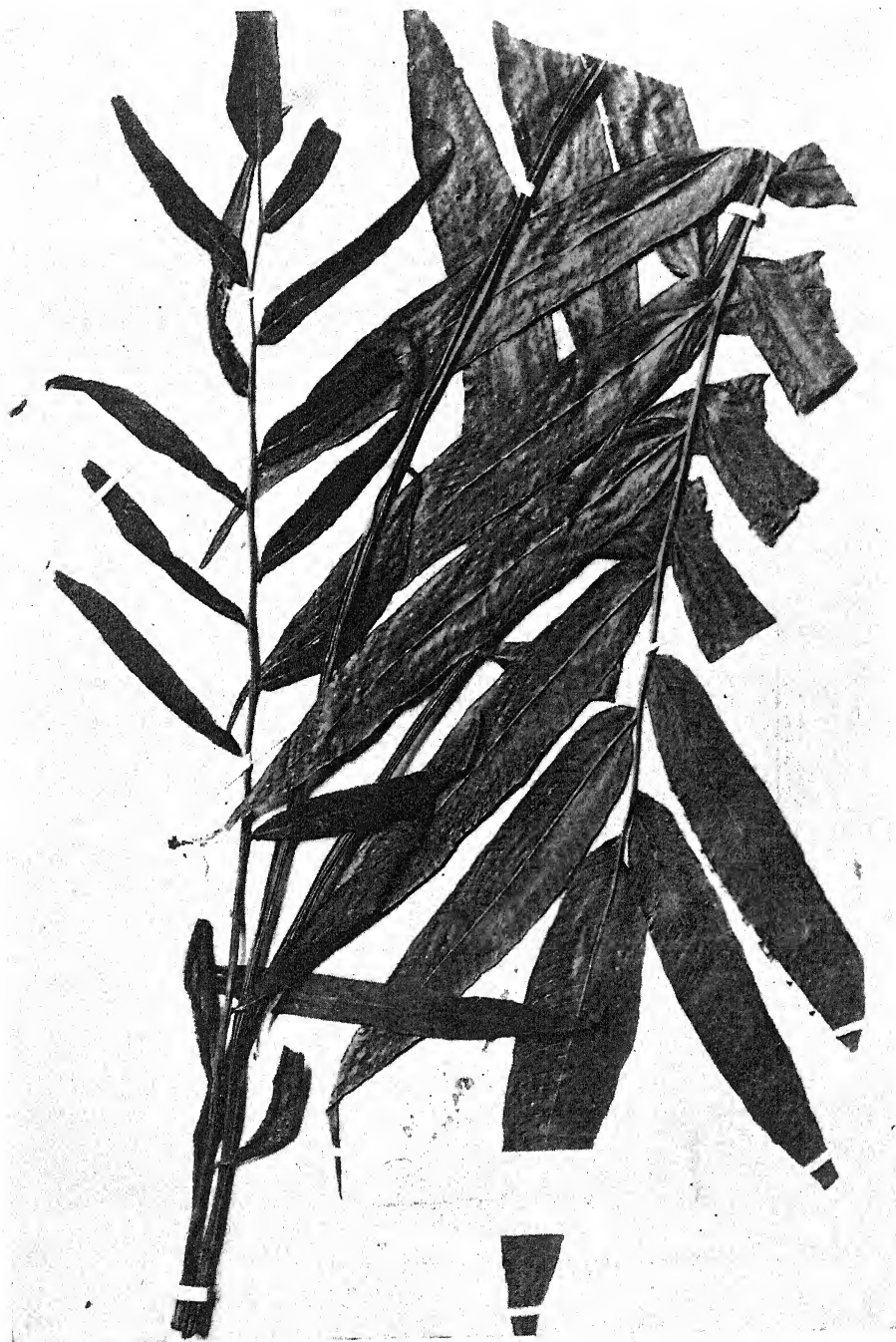
13. *Dryopteris nesiotica* Maxon & Morton, sp. nov.

PLATE 12

Rhizoma deest. Folia rigide suberecta, usque ad 95 cm. longa, subbiformia, stipitibus validis, pallide brunneis, profunde et anguste sulcatis, cum rhachi minute puberulis, eis foliorum steriliū quam laminis multo brevioribus, eis fertiliū laminas subaequantibus; lamina 1-pinnata; pinnae 9-11-jugae et terminalis conformis, adscendentes, integrae, inferiores plurimae suboppositae, ceterae alternae. Laminae steriles ambitu late oblongae, 40-55 cm. longae, ca. 30 cm. latae; pinnae subaequales, 16-22 cm. longae, 2.5-3 cm. latae, late lineares, parte apicali longe attenuatae, basi obtusae vel rotundatae, vel superiores antice obliquae, hae postice plus minusve adnatae, ceterae sessiles (infimae brevissime petiolulatae exceptae); venae laterales infra acuminem ca. 40-jugae, spatio 3 cm. ca. 8, sub angulo 60°-70° egredientes, leviter falcatae, fere glabrae, utrinque prominulae; venulae leviter curvatae, sub angulo 45° eductae, inaequales, angulo subrecto conjunctae, utrinque prominulae; areolae 9-11-seriatae, breves, venulis excurrentibus brevibus. Laminae fertiles oblongae; pinnae remotae, lineares, 9-13 cm. longae, attenuatae, basi inaequaliter subcuneatae, sessiles (superiores semiadnatae exceptae); sporangia glabra, areolarum arcum totum insidentia, creberrima et numerosissima, pinnae pagina inferiori (costa excepta) suffusa.

Explanation of Plate 12

Plate 12. *Dryopteris nesiotica* Maxon & Morton, sp. nov. The type specimen; Trinidad, *Jenman*. About half natural size.



MAXON & MORTON: DRYOPTERIS



Type in the herbarium of the New York Botanical Garden, collected in Trinidad by G. S. Jenman, together with a second specimen which is evidently of the same collection.

The present species is allied to *D. angustifolia*, but is at once distinguished by its broad sterile pinnae, which except for the basal pair are neither stalked nor cuneate, and by its distant lateral veins.

14. *Dryopteris dispar* Maxon & Morton, nom. nov.

*Meniscium affine* Presl ex Ettingsh. Denkschr. Akad. Wiss. Math. Naturw. (Wien) 23: 94. pl. 13, fig. 3. 1864; Farnkr. Jetztw. 170. fig. 73; pl. 135, fig. 16. 1865. Not *Dryopteris affinis* Newm. 1854.

Since its original publication this species, from "Brazil," has remained unknown, having been described inadequately on characters of venation only and without citation of specimens. We give here an amplified description:

Stipe about equaling the blade, slender (2 mm. in diameter), stramineous, lustrous, glabrous; blades imparipinnate, oblong in outline, 50 cm. long, 20 cm. broad, the rachis stramineous, lustrous, glabrous; pinnae 9-jugate, subopposite, membranous, linear-falcate, up to 14.5 cm. long and 1.7 cm. wide, acuminate-attenuate in apical fourth, subsessile, at base obtuse and rounded-auriculate on both sides; margins subentire; leaf surface, costae, and veins glabrous except for scattered whitish stipitate glands, the lateral veins about 11 pairs in the space of 3 cm.; venules almost straight, meeting each other at an obtuse angle, the areoles 4-6-seriate; sori not confluent; sporangium stalk setose.

The above description is drawn from a specimen in the Kew Herbarium collected on bank of the Río Mauhy, in the state of Amazonas, Brazil, by J. W. H. Traill (no. 1402). It does not agree exactly with the plate of Ettingshausen, for in that the areoles are only 3- or 4-seriate and the bases of the pinnae not auriculate. In the present specimen the areoles are mostly 5-seriate. However, since no other species has so few areoles and the plants otherwise are in close general agreement, we believe the identification to be correct.

15. *DRYOPTERIS SIMPLICIFRONS* C. Chr. Ind. Fil. 486. 1906.

*Meniscium giganteum* Mett. Fil. Lechl. 1: 19. 1856.

*Phegopteris gigantea* Mett. Fil. Lechl. 2: 22. 1859.

*Nephrodium giganteum* Diels in Engl. & Prantl, Pflanzenfam. 14: 177. 1899; not Baker (1867), Baker (1874), nor Cesati (1877).

*Dryopteris gigantea* C. Chr. Ind. Fil. 267. 1905; not Kuntze (1891).



This well-known species, founded on material from St. Gavan, Peru (Lechler 2292), is at once recognized by its large simple fronds. Christensen intimates that pinnately divided forms are found, but we have seen no specimens so named nor any that can be referred to this species. Such material would very likely be referable to *D. Andreana* or *D. membranacea*. The closer relationship of *D. simplicifrons* is undoubtedly with the latter, with which it agrees in having appendages borne on the stalk of the sporangium. In *D. membranacea* these are in the form of sharply pointed hyaline setae, whereas those of *D. simplicifrons* are stalked capitate glands. The stalk of the gland is often rather long, and the gland itself is large, spherical and of a dark red color. At first these glands are very conspicuous among the sporangia, but they appear to be readily deciduous and are not to be seen on older specimens.

Unfortunately the specific name *gigantea*, being preoccupied for an Old World *Tectaria*, can not be retained for the present species, the "new combination" *Dryopteris gigantea* (Mett.) C. Chr. having been published in spite of *Dryopteris gigantea* Kuntze (1891), which is listed on the same page. In a succeeding fascicle of the Index Filicum (p. 486), which appeared the next year (1906), the new name *Dryopteris simplicifrons* is validly published by Christensen as the equivalent of *Phegopteris gigantea* Mett. and this, though it has subsequently been ignored by Christensen himself and by other writers, must now be taken up.

*Dryopteris simplicifrons* inhabits dense humid forests, from lower altitudes to about 1500 meters. It ranges from Costa Rica to Peru, but is yet to be found in Panama. The following specimens have been studied:

COSTA RICA: Forest above Tsaki, Talamanca, alt. 500 meters, *Tonduz* 9448. Peralta, alt. 600-700 meters, *Lankester*. Without locality, *Werckle*.

COLOMBIA: Along Río Guatapé, Dept. Antioquia, alt. 1040 meters, *Kalbreyer* 1453 (K). "Ciñegetas," Dept. Antioquia, alt. 1200-1500 meters, *Kalbreyer* 1865 (K). Along Río Timbiquí, near Coteje, Dept. Cauca, alt. 100-500 meters, *Lehmann* 8946 (K, US); also *Lehmann* as B. T. 444 (K, US).

ECUADOR: Forests at 300-1200 meters, Aug. 1875, *Sodirol* 54 (K, 3 sheets).

PERU: St. Gavan, in shady wet forests, *Lechler* 2292, type coll. (K). Pichis Trail, San Nicolas, Dept. Junín, alt. 1100 meters, *Killip & Smith* 26018 (US).

16. DRYOPTERIS MEMBRANACEA (Mett.) C. Chr. Ind. Fil. Suppl. 35. 1913.

PLATE 13

*Phegopteris membranacea* Mett. Fil. Lechl. 2: 22. 1859.

*Nephrodium Lechleri* Hieron. Bot. Jahrb. Engler 34: 448. 1904.  
*Dryopteris Lechleri* C. Chr. Ind. Fil. 274. 1905.

*Phegopteris membranacea* was described by Mettenius with citation of two Peruvian specimens collected by Lechler, viz. (1) no. 1785, from Azangaro, which he had previously listed<sup>17</sup> as *M. reticulatum*, and (2) an unnumbered specimen from St. Gavan. His description is ample and clearly applies to the species subsequently described as *Nephrodium Lechleri* by Hieronymus, who based his description upon *Lechler* 1785, from Azangaro, and *Lechler* 2321, from St. Gavan, the latter being presumably the second specimen cited by Mettenius as *P. membranacea*. In so doing Hieronymus appears to have regarded the Berlin material as an aggregate and to have fallen into the error of selecting typical *membranacea* for description as a new species, wrongly applying the name *membranacea* to another Lechler specimen from St. Gavan, viz. no. 2493. A photograph of no. 2493 has kindly been forwarded from Berlin. It shows a large sterile blade, with nine pairs of pinnae below the greatly enlarged *pinnatifid* apex. The specimen thus disagrees widely with Mettenius' description, does not bear an annotation by him, and certainly was not included in his *original* concept of *P. membranacea*. If not actually teratological, it is at least highly atypical for any known member of this genus and can not at present be placed specifically.

Thus, *Nephrodium Lechleri* and *Dryopteris Lechleri* are exactly the equivalent of *D. membranacea* and, having been based on the same specimens as that, are illegitimate. Technically, according to Article 60 of the International Rules of Nomenclature, they may be disregarded.

We have seen only the following specimens, though Hieronymus lists this species (as *D. Lechleri*) from Ecuador on the basis of *Stübel* 1002.

COLOMBIA: Between Pueblo Viejo and San Miguel, Dept. Magdalena, alt. 900–1700 meters, *Seifríz* 556 (US).

PERU: In rupibus umbrosis prope Azangaro, *Lechler* 1785, type coll. (K, 2 sheets). Mishuyacu, near Iquitos, alt. 100 meters, in forest, *Klug* 200 (US); *Klug* 1533 (US, Y). Chazuta, Río Huallaga, Dept. San Martín, alt. 260 meters, in forest, *Klug* 3970 (US, Y). Mt. Campana, near Tarapoto, *Spruce* 4645 (K, US).

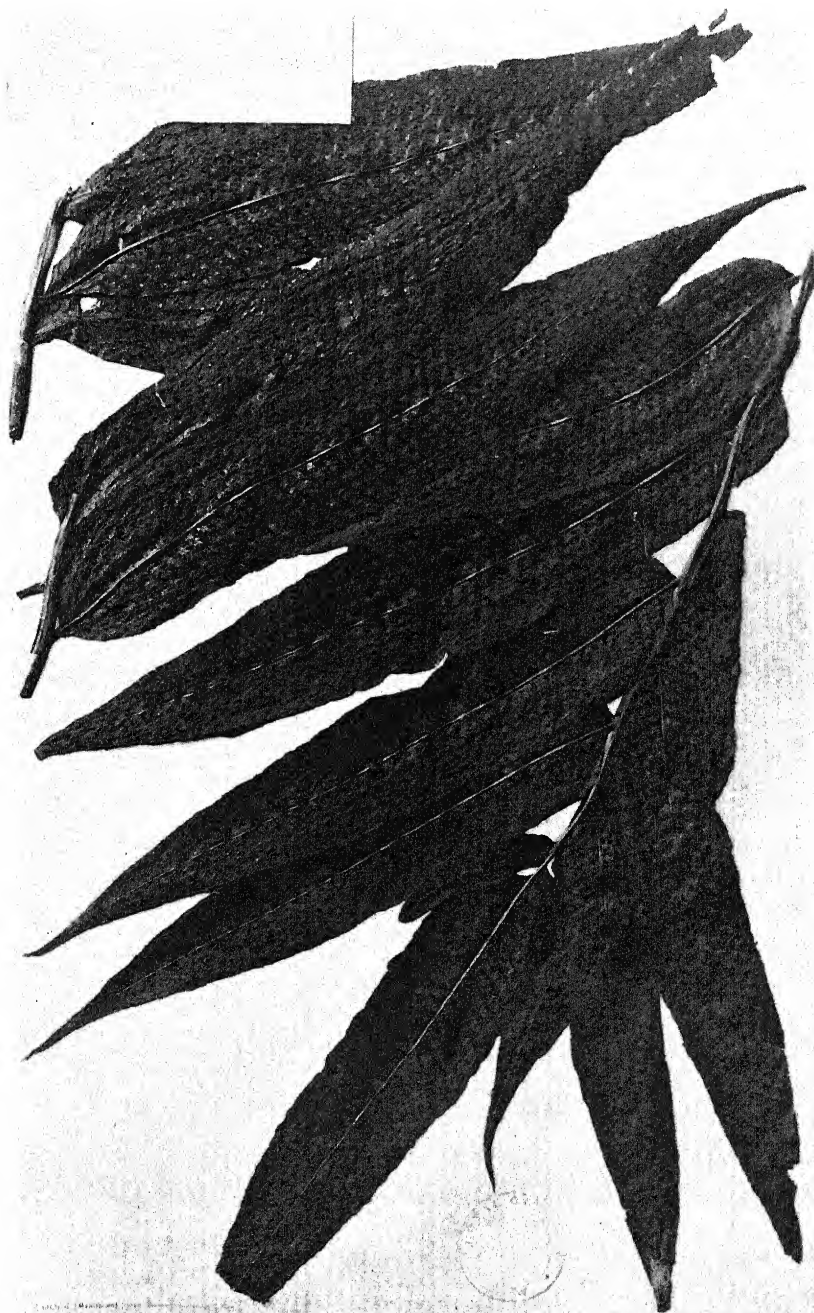
Reference of the last collection to *D. membranacea* is somewhat doubtful, on account of its conspicuously strigose costae and veins. The speci-

<sup>17</sup> Fil. Lechl. 1: 19. 1856.

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#### Explanation of Plate 13

Plate 13. *Dryopteris membranacea* (Mett.) C. Chr. Isotype specimen, at Kew; Peru, *Lechler* 1785. About half natural size.



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mens are very immature, however, and are only slightly more hairy than one of the two specimens of *Lechler* 1785, this also being very young, with most of the sporangia undeveloped.

17. *Dryopteris Standleyi* Maxon & Morton, sp. nov.

Rhizoma deest. Folia conformia, rigide suberecta, usque ad 1.9 m. longa, stipitibus validis, quam laminis multo longioribus, e basi fusca pallide brunnescentibus vel ochraceo-stramineis, obtuse angulatis, minute et laxe puberulis; lamina 1-pinnata. Laminae steriles late oblongae, usque ad 50 cm. longae et 40 cm. latae, apice acutiusculae vel abrupte acutae; pinnae 12–17-jugae et terminalis conformis, subpatentes, subimbricatae, margine subintegrae vel leviter repandae, pleraeque superiores sensim minores, ceterae subaequales, ligulatae, 12–22 cm. longae, 2.5–4 cm. latae, apice acutae vel attenuatae, basi late rotundatae vel pleraeque subcordatae, omnes sessiles; venae laterales spatio 3 cm. 9–13, sub angulo 60° egredientes, utrinque prominulae, subtus cum venulis pilis curvatis brevibus paucis praeditae; venulae sub angulo 35°–40° eductae, longae, acutissime conjunctae; areolae 9–14-seriatae, breves, profunde antice curvatae, venulis excurrentibus plerumque longis sed liberis; parenchyma chartacea, pilis rigidis parvis hinc inde praedita, mox glabrescens. Laminae fertiles anguste oblongae, usque ad 70 cm. longae et 40 cm. latae, apice abrupte acutae; pinnae obliquae, ca. 17-jugae et terminalis, sterilibus similes sed plerumque angustiores (maximae 22 cm. longae et 2.5–4 cm. latae), apice attenuatae, basi non reductae, sessiles, margine irregulariter sinuatae vel crenatae, superiores paulum minores; venae laterales spatio 3 cm. 13–15, sub angulo 75° egredientes, prominulae, subtus cum venulis pilos breves paucos ferentes; venulae sub angulo ca. 45° eductae, rectae, angulo obtuso conjunctae, venulis excurrentibus liberis hydathoidis linearibus terminatis; areolae 11–14-seriatae, dimidiis trapeziformibus; sori magni, late oblongi, crebri, aetate confluentes, sporangiorum pedicellis setis rigidis solitariis vel binis supra instructis.

Type in the U. S. National Herbarium, nos. 1,150,894–6, representing two complete fronds (fertile and sterile), collected on a brushy bank near Quiriguá, Dept. Izabal, Guatemala, altitude 75 to 225 meters, May 15–31, 1922, by Paul C. Standley (no. 24126). Other specimens examined are as follows:

MEXICO: Cerro de Tonala, in a forest ravine, *C. & E. Seler* 2013 (US).

COLOMBIA: Near Onaca, Santa Marta, alt. 750 meters, boggy situations in "open land" ravines, *H. H. Smith* 2458, 7 specimens (F, US, Y).

PERU: Zepelacio, near Moyobamba, Dept. San Martín, alt. 1100 to 1200 meters, *Klug* 3354 in part (U. S.).

BOLIVIA: San Carlos, Mapiri region, alt. 850 meters, *Buchtien* 228 (G).

Closely related to the present species is a form from Taboga Island, Panama (*Killip* 2642; *Standley* 28025), which very likely is specifically

distinct. It is similar in venation but is definitely pilosulous beneath, in strong contrast to the essentially glabrous leaf tissue of *D. Standleyi*. The Killip specimen is remarkable also for its widely distant pinnae.

18. *Dryopteris Hostmanni* (Klotzsch) Maxon & Morton, comb. nov.

PLATE 14

?*Meniscium arborescens* Humb. & Bonpl.; Willd. Sp. Pl. 5: 133. 1810. Not

*Dryopteris arborescens* Kuntze (1891).

*Polypodium Hostmanni* Klotzsch, Linnaea 20: 397. 1847.

*Meniscium Kapplerianum* Fée, Gen. Fil. 224. 1852.

?*Phegopteris arborescens* Mett. Fil. Lechl. 2: 24. 1859.

?*Dryopteris reticulata* var. *arborescens* Brause, Verh. Bot. Ver. Brand. 51: 2. 1910.

*Polypodium Hostmanni* Klotzsch was described from Surinam upon material collected by Hostmann and Kappler (no. 828), and the same number served also as the sole basis of *Meniscium Kapplerianum* Fée. Whether *Meniscium arborescens* Humb. & Bonpl. is the same appears to be highly problematical. Not only Humboldt and Bonpland but Mettenius, who saw the plant in cultivation, describe it as arborescent. In the specimens of *D. Hostmanni* that we have seen there is no evidence of such a development, otherwise unknown in *Meniscium*; yet Hieronymus also regarded *arborescens* and *Hostmanni* as synonymous. In any case, the name *arborescens* is not available, being preoccupied by *Dryopteris arborescens* (Baker) Kuntze, 1891, applied to a Samoan plant.

The specimens cited below are of uniform facies, one of the largest being a frond collected by Jenman, in which the pinnae are 2 to 2.5 cm. broad. Sporangium setae are conspicuous in all.

PANAMA: Río Cañazas, Prov. Veraguas, Allen 164 (US).

DUTCH GUIANA: In sylvis humidis, *Hostmann & Kappler* 828, type coll. (B, K, Y). Without locality, *Wulfschlaegel* (F, Y).

BRITISH GUIANA: Pirana, *Appun* 1469 (K). Rockstone, in dense upland forest, *Gleason* 609 (US, Y). Demerara River, *Jenman* (Y, 2 sheets); *Jenman* 3845 (K).

19. *Dryopteris Desvauxii* Maxon & Morton, nom. nov.

*Meniscium longifolium* Desv. Mém. Soc. Linn. Paris 6: 223. 1827.

*Meniscium longifolium* Fée, Crypt. Vasc. Brés. 1: 84. pl. 25, fig. 2. 1869.

*Nephrodium longifolium* Hieron. Bot. Jahrb. Engler 34: 449. 1904.

*Dryopteris longifolia* (Fée) Hieron. Hedwigia 46: 351. 1907.

*Dryopteris reticulata* var. *longifolia* (Desv.) Rosenst. in Buchtien, Contr. Fl. Bol. 1: 44. 1910.



The present species offers an unusual problem in nomenclature, recently discussed by Mr. C. A. Weatherby<sup>18</sup> in his paper on the ferns proposed by Desvaux as new. Both Desvaux and Fée described independently this fern under the same name, *Meniscium longifolium*, but upon different material. Fée's name is a later homonym, yet Hieronymus in transferring the species to *Dryopteris* used it, rather than the *longifolium* of Desvaux. Since Fée's epithet is illegitimate, the new combination made by Hieronymus under *Dryopteris* is equally so; nevertheless it makes impossible the transfer now of the epithet given by Desvaux. A new name must therefore be given, as above.

As here considered *D. Desvauxii* shows great variability. It is close to *D. permollis*, though typical specimens of the two are quite different. Usually it is a much larger plant, with longer-stalked pinnae, and a shorter less dense pubescence. Especially noteworthy is the presence of stalked capitate glands, which normally replace the hairs of the leaf surface to a considerable extent. In some specimens all the hairs are replaced by glands, in which case the plants appear so different that their formal recognition seems desirable. The following specimens of the typical form have been examined:

BRAZIL: State of Amazonas: Manaus, Gleason 11 (Y); Barra do Rio Negro, Spruce 1243 (K); near San Gabriel, along Rio Negro, Spruce 2141 (K, US). State of Para: Near Gurupatuba, west of Monte Alegre, Traill 1403 (K). State of Ceara: Serra de Araripa, Gardner 1904 (K). State of Goyaz: Glaziou 22633 (B, K). State of Espirito Santo or Bahia: Blanchet 3984 (C, K). State of Minas Geraes, Regnell III. 1444 in part (US). Rio de Janeiro: Organ Mts., Gardner 103 (K); Valence, Glaziou 1747, type coll. of *M. longifolium* Fée (C, K, US); without definite locality, Glaziou 2375, paratype coll. of *M. longifolium* Fée (C, K); Petropolis, Spannagel 523 (Y). State of Paraná: Jacarehy, Dusén 6580 (B, F, US); Serra do Mar, Porto de Cima, Dusén 14679 (C, F); Alexandra, Dusén 10159 (B, K, US), 15258 (F). State of Santa Catharina: Joinville, etc. Schmalz, partly as no. 166 (F, US, Y). Without locality, Burchell 2635 (K); Glaziou 15743 (C), 15745 (C).

BOLIVIA: San Antonio, near Mapiri, Buchtien 1063 (US). Roboré,

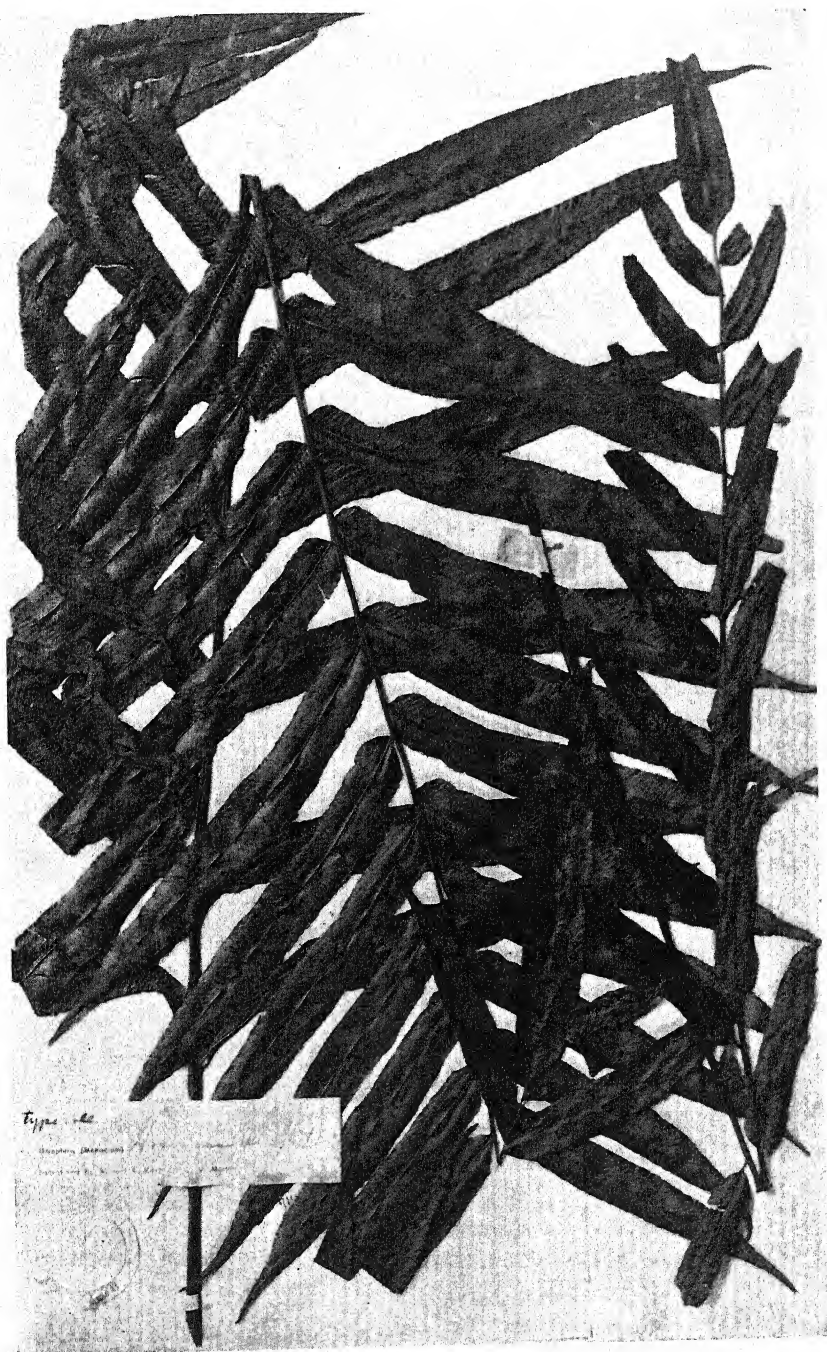
<sup>18</sup> Contr. Gray Herb. 114: 27. 1936. A photograph of Desvaux's type specimen has very kindly been furnished by Mr. Weatherby.

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#### Explanation of Plate 14

Plate 14. *Dryopteris Hostmanni* (Kl.) Maxon & Morton. Isotype specimen, at Kew; Dutch Guiana, Hostmann & Kappler 828. About half natural size.





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Cárdenas 2991 (US). Buena Vista, Dept. Santa Cruz, *Steinbach* 5312 (US). San José, *R. S. Williams* 1245 (US, Y).

19a. *Dryopteris Desvauxii* f. *glandulosa* Maxon & Morton, forma nov.

Lamina pilis destituta, glandulis stipitatis capitatis albidis instructa.

Type in herbarium of the New York Botanical Garden, collected at Morro das Pedras, São Paulo, Brazil, February 1928, by Brade (no. 5753). Other specimens examined are as follows:

BRAZIL: State of Goyaz, *Glaziov* 22632 (F, Y). State of São Paulo: Santos, *Lindberg* 545 (K). State of Paraná: Alexandra, *Dusén* 15258 (US).<sup>19</sup>

BOLIVIA: Mapiri, alt. 480 meters, *R. S. Williams* 1281 (Y).

PERU: Mishuyacu, near Iquitos, Dept. Loreto, alt. 100 meters, *Klug* 509 (US).

20. *Dryopteris permollis* Maxon & Morton, nom. nov.

*Phegopteris mollis* Mett. Ann. Sci. Nat. V. Bot. 2: 242. 1864. Not *Dryopteris mollis* (Jacq.) Hieron. 1907.

*Nephrodium sorbifolium* var. *molle* f. *angustipinnata* Hieron. Bot. Jahrb. Engler 34: 449. 1904.

*Dryopteris sorbifolia* var. *mollis* Hieron. Hedwigia 46: 351. 1907.

This species, as *Phegopteris (Meniscium) mollis*, was well described by Mettenius upon material from Llano de San Martín, Paraiso, Colombia, alt. 300 meters, collected by Triana. It was reduced to varietal rank by Hieronymus under both *Nephrodium sorbifolium* and *Dryopteris sorbifolia*; but *Meniscium sorbifolium* is exactly synonymous with *D. reticulata*, as discussed under that species, and is not closely related to the present plant. Mettenius' epithet, *mollis*, being preoccupied under *Dryopteris*, a new one is required.

Usually *D. permollis* is readily recognized by its densely soft-pilose under surfaces. Capitate glands are sometimes found among the hairs, but not so commonly as in *D. Desvauxii*. The following specimens have been examined:

COSTA RICA: Buenos Aires, in forest along the Río Ceibo, *Pittier* 4852 (US).

COLOMBIA: Type collection, *Triana* (US). Cali, *André* 429 (F, K, US, Y); *Lehmann* 2937 (K, US). Intendencia del Chocó, along Río Atrato, *Archer* 1808 (US). Río Pauca, *Dryander* 631 (US). Buenaventura, Dept.

<sup>19</sup> A specimen of this number (with identical data) in Field Museum is typical *D. Desvauxii*.

El Valle, *Killip* 11683 (US); *Pennell & Killip* 5295 (US, Y). Mesa de los Santos, Dept. Santander, *Killip & Smith* 15248 (US, Y). Villavicencio, *Pérez* 10 (US). San Carlos, Dept. Antioquia, *Kalbreyer* 1376 (K).

BRITISH GUIANA: Marima, *Appun* 1058 (K).

PERU: Pampayacu, *Kanehira* 129 (US).

BOLIVIA: San Carlos, near Mapiri, *Buchtien* 241 (Y). Antahuacana, *Buchtien* 2210 in part (US). Ticunhuaya, *Tate* 1062 (Y).

The altitudinal range is from sea level to about 1500 meters.

To this species is perhaps to be referred a specimen in the Kew Herbarium collected at Tovar, Venezuela (*Fendler* 232 in part), in which almost all the hairs are suppressed, the veins being conspicuously stipitate-glandular.

21. *Dryopteris chrysodioides* (Fée) Maxon & Morton, comb. nov.

*Meniscium chrysodioides* Fée, Gen. Fil. 225. 1852.

Fée's description is brief and is followed by the statement, "Habitat in America australi. (Collect. Pamplin., in Herb. cl. Mougeot., no. 55," neither the country nor collector being indicated.<sup>20</sup> This species has never before been placed very definitely, being listed in the Index Filicum as a synonym of *D. reticulata*; but upon reading Fée's comment, "aspectu *Chrysodii vulgaris*," it occurred to us independently to associate the name with several British Guiana specimens collected by Jenman, which indeed bear a general resemblance to *Acrostichum aureum* (*Chrysodium vulgare*). They agree well with Fée's description and represent a very well marked species, which presumably attains a greater size than indicated by the description or by Jenman's specimens. These are as follows:

BRITISH GUIANA: Pomeroon River, *Jenman* 2072 (K); *Jenman* s. n. (Y, 2 sheets). Mazaruni River, *Jenman* in 1881 (Y).

Of this species the following is a well-marked variety. It is based on

<sup>20</sup> The following comment on Fée's statement is obligingly furnished by Dr. J. H. Barnhart: "I understand by this that the Mougeot Herbarium contained a collection distinguished as the 'Collectio Pampliniana' and that the specimen in question was either no. 55 of that collection or had had that number assigned to it by Mougeot. The only botanist by the name of Pamplin known to me is William Pamplin, who was an Associate of the Linnaean Society for almost 70 years, and died in 1899 in his ninety-third year. For 23 years (1839-62) he was a book dealer in London, specializing in botanical books, and it would not be at all strange if Mougeot received from him either by gift, exchange, or purchase a collection of botanical specimens. I do not think that Pamplin was ever in any part of America. He traveled all over Great Britain, studying its flora, but I have no evidence that he even crossed the Channel to the Continent." To this Mr. C. A. Weatherby adds that Pamplin's herbarium was purchased by G. C. Druce and is presumably at Oxford University.

*Glaziou* 22631, which Christensen mentioned as probably representing an undescribed species.

21a. *Dryopteris chrysodioides* var. *goyazensis* Maxon & Morton, var. nov.

Filix maxima, pinnis alternis multijugis ligulatis, sterilibus usque ad 40 cm. longis et 7 cm. latis subintegris acuminatis basi rotundatis breviter petiolulatis subtus praecipue in venis breviter pilosulis, venis primariis 5 vel 6 in spatio 3 cm., venulis subsigmoideis, areolis 16-19-seriatis, pinnis fertilibus minoribus usque ad 23 cm. longis et 4.5 cm. latis margine crenatis subtus dense pilosis; sori confluentes; sporangiorum pedicellus apice setosus.

Type in herbarium of the New York Botanical Garden, collected in the valley of the Rio Corumba, State of Goyaz, Brazil, July 23, 1894, by M. A. Glaziou (no. 22631). Duplicates of this collection are at Copenhagen and Field Museum. Other specimens are as follows:

BRITISH GUIANA: *Appun* 844 (K, 3 sheets).

BRAZIL: State of Bahia, *Blanchet* 1023 (Y). Matto do Curupira, State of Matto Grosso, *Lindman* A 3043 (US). Without locality, *Riedel* 59 (US).

This variety differs from the typical form of *D. chrysodioides* in its larger and more numerous sterile pinnae and in its strongly crenate fertile pinnae. From *D. membranacea*, which in some ways it resembles, it differs in having the fertile pinnae smaller than the sterile and conspicuously crenate, and in its confluent sori.

DOUBTFUL AND EXCLUDED SPECIES

MENISCIUM CRISTATUM Desr. in Lam. Encycl. 4: 94. 1797.

This is *Diplazium cristatum* (Desr.) Alston, Journ. Bot. Brit. & For. 74: 173. 1936.

MENISCIUM FENDLERI Eaton ex C. Chr. Ind. Fil. 421. 1906.

According to Christensen the citation is Bot. Gaz. 3: 89. 1878, but no such name appears at this place. The species is *Bolbitis macrophylla*.

MENISCIUM GUYANENSE Fée, Gen. Fil. 224. 1852.

This is *Bolbitis macrophylla*.

MENISCIUM "PUNCTA LUNULATUM Rich." ex C. Chr. Ind. Fil. 421. 1906.

At the place cited by Christensen, viz., Act. Soc. Hist. Nat. (Paris) 1: 114. 1792, this is by no means intended as a species name but is merely the first part of the generic description of *Meniscium* given by Richard.

**Bolbitis macrophylla** (Kunze) Maxon & Morton, comb. nov.

*Meniscium macrophyllum* Kunze, Flora 22<sup>1</sup>: Beibl. 44. 1839.

*Heteroneuron meniscioides* Fée, Hist. Acrost. 93. pl. 55. 1845.

*Poecilopteris meniscioides* Presl, Epim. Bot. 175. 1851.

*Meniscium guyanense* Fée, Gen. Fil. 224. 1852.

*Phegopteris macrophylla* Mett. Fil. Lechl. 2: 24. 1859.

*Nephrodium macrophyllum* Keys. Pol. Cyath. Herb. Bung. 48. 1873.

*Acrostichum Fendleri* Baker, Journ. Bot. Brit. & For. 25: 100. 1887.

*Meniscium oligophyllum* Hort. ex Baker, Ann. Bot. 5: 487. 1891.

*Leptochilus Fendleri* C. Chr. Bot. Tidsskr. 26<sup>2</sup>: 285. 1904.

*Dryopteris macrophylla* C. Chr. Ind. Fil. Suppl. I. 35. 1913.

*Dryopteris anceps* Maxon, Contr. U. S. Nat. Herb. 24: 62. 1922.

Close study of a large series of specimens convinces us that this species may not be retained in *Dryopteris*. The sporangia are not borne on a definite receptacle, as in all species of that genus, but are regularly distributed over the whole leaf surface. A few species of *Meniscium*, such as *D. chrysodioides*, are so heavily fertile that in age the sporangia appear to cover the whole leaf surface, but a careful dissection shows that the stalks always arise on the arcuate cross-veins and never from the leaf tissue between the veins.

In the Trinidad specimens and in most of those from British Guiana the sporangium wall is conspicuously setose. This is not true for most of the Brazilian material. However, this variation is not found to be correlated with other differences, and we regard the entire series of specimens as conspecific.

The genus *Leptochilus* Kaulf.<sup>21</sup> is at present restricted by Ching and Christensen to a small group of Old World species considered to be of polypodioid rather than dryopteroid affinity. Most of the species formerly included in *Leptochilus* they place in *Bolbitis* Schott.<sup>22</sup> Within the latter polymorphic genus, as represented in tropical America, the present species is quite isolated by reason of its entirely meniscioid venation. None of the other American species have this venation, although an approach is found in several Old World species, notably in *B. subcrenata* (Hook & Grev.) Ching, of India and Ceylon. In that the venation is sometimes entirely meniscioid, although commonly the basal areole bears more than one excurrent venule. In other respects, however, *B. subcrenata* is widely different from our plant. The sterile blades of *B. macrophylla* resemble very strongly those of *Dryopteris chrysodioides*, but may be distinguished by their glabrous rather than hirsutulous rachises and their glabrous leaf tissue.

<sup>21</sup> Enum. Fil. 147. 1824.

<sup>22</sup> Gen. Fil. pl. 14. 1834.



*Bolbitis macrophylla* is rather widely distributed, and we have examined the following specimens:

TRINIDAD: L'Orange Road, *Homersley* 226 (US). Brazil, *Britton*, *Britton*, & *Freeman* 2142 (US). Without specific locality, *Bot. Gard. Herb.* 1584 (US); *Fendler* 88, type of *Acrostichum Fendleri* (US, Y).

TOBAGO: Between Roxborough and Parlatuvier, *Broadway* 4904 (US).

BRITISH GUIANA: Barina River, *Jenman* (Y). Demerara River, *Jenman* (Y). Potaro River, *Jenman* 1449 (K). Without special locality, *Jenman* 2072 (K); *Appun* 732 (K).

FRENCH GUIANA: Acarouany (or Karouany), *Sagot* 1396 (B, K). Menonicia, *Leprieur* 70 (US).

BRAZIL: Serra do Mar, near Ilhéos, Bahia, *Martius* 363, type coll. (K, Y); *Blanchet* 2228 (K), 2477 (K). Bahia, *Luschmuth* 82 (B). Para, *Pételot* (F). Tanaii, *Spruce* 32\*\* (K). Sa do Mar, São Paulo, *Wacket* 211 (Y). Without special locality, *Riedel* 1292b (B); *Riedel* s. n. (C); *Riedel* 59, form with simple blades (US); *Glocker* s. n. (US).

PERU: Pongo de Manseriche, Loreto, *Mexia* 6202 (US).

VENEZUELA: Base of Mt. Cocui, *Spruce* 3030 (K).

*MENISCIMUM OPACUM* Baker, *Journ. Bot. Brit. & For.* **15**: 166. 1877.

As stated in the introduction this species, properly known as *D. Christii* C. Chr., belongs to the subgenus *Stigmatopteris*.

*MENISCIMUM SALICIFOLIUM* Presl, ex Ettingsh. in *Denkschr. Akad. Wiss. Math. Naturw. (Wien)* **23**: 93. 1864; Ettingsh. *Farnkr. Jetzw.* 169. *pl.* 132, *figs.* 2, 7. 1865 (non Wall. ex Hook. 1854).

Described from Brazil on characters of venation only. We are unable to identify the figure definitely, though it suggests *Dryopteris Salzmanni*. The plant is utterly different from the Old World *salicifolium* of Wallich, under which it is cited in the *Index Londinensis*.

UNITED STATES NATIONAL MUSEUM,  
WASHINGTON, D. C.



## The Taxonomy of a Community of Blue-Green Algae in a Minnesota Pond

HELEN FOOT BUELL

(WITH TWELVE FIGURES)

In a previous paper (Buell, 1938) the author described a fresh-water community of blue-green algae in Minnesota. In its early stages it is benthic in ooze in water 10 to 20 feet deep. Later it floats to the surface, buoyed up by gases liberated within the mass during photosynthesis.

This community is a globular mass whose outer portion is a thin, compact tegument composed almost exclusively of species of Oscillatoriaceae. The trichomes are arranged with their long axes parallel to the vertical axis of the mass. This tegument encloses a soft, oozy portion, forming the bulk of the mass. In this ooze are found chiefly unicellular pseudo-vacuolate Cyanophyceae.

The present paper is devoted to the Cyanophycean members of this community. Detailed discussions are given only of those forms believed to be new to science or which are otherwise significant.

### METHODS

In the field small pieces of material were removed from different parts of the mass, in order to determine regional distribution of forms, and were preserved immediately in 3-4 per cent commercial formalin. Observations were also made on living material in order to offset any artifacts produced by the action of the preservative. The drawings were made from glycerine or glycerine gelatine mounts. Most of the figures were drawn to scale according to Tilden's (1934) method, and, with two exceptions, are reproduced at a magnification of 1000.

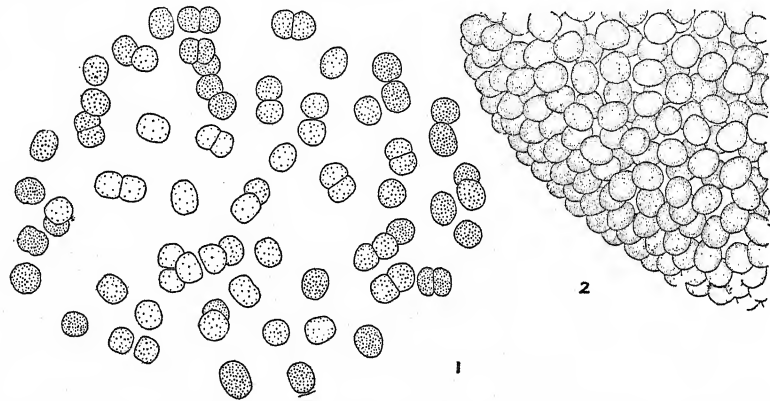
The type specimens have been deposited in the phycological laboratory of the botany department at the University of Minnesota.

### CHROOCOCCACEAE

*Microcystis pulverea* (Wood) Migula (fig. 1) is found rarely in the interior portion of most communities. The size of the cells is from  $1.6-2.0 \times 1.6-2.6\mu$ , with an average of  $1.7 \times 2.0\mu$ . Authors (Wolle, 1887; Lemmermann, 1907; Forti, 1907; Tilden, 1910; Smith, 1920; Crow, 1923; Geitler, 1925, 1932) have described the cells of *M. pulverea* as ranging in size from 2 to  $3\mu$ . Lemmermann (1907), in establishing *M. incerta*, gave its size as  $1-1.5\mu$ , while Smith (1920) places the size at  $1-2\mu$ . Smith also states that since the difference between *M. pulverea* and *M. incerta* is "mainly one of

size it might be better to consider *M. incerta* a variety of *M. pulverea*." Crow (1923), following Smith's suggestion, says, "it therefore seems that the essential difference between the two forms is one of size and as it is not customary to establish species on this character alone we have regarded *M. incerta* as a variety of *M. pulverea*." Geitler accepts Crow's decision. However, in view of the fact that the sizes for species and variety are continuous, i.e.,  $1-2\mu$  and  $2-3\mu$ , and also in view of the fact that the cells described here are intermediate in size between them, it seems better to consider *M. incerta* as synonymous with *M. pulverea*, the size range for the species then being  $1-3\mu$ .

*Microcystis* spp. In the interior of the community the dominant algae are pseudo-vacuolate species of *Microcystis*. These become very abundant



Figs. 1-2. Fig. 1. *Microcystis pulverea* (Wood) Migula.  $\times 1000$ . Fig. 2. *Coelomorion regularis* H. F. Buell spec. nov. One fourth of colony, surface view.  $\times 1000$ .

during the hot weather of August; a single microscope mount may show hundreds of colonies. Crow (1923) says, "whenever abundant material occurs the precise limits of the different species become impossible to define." The Minnesota material illustrates this fact, intergrading colony forms occurring between all the species present. The following species are definitely present: *M. protocystis* Crow, *M. viridis* (A. Braun) Lemm., *M. flos-aquae* (Wittr.) Kirchn., *M. marginata* (Menegh.) Kütz., and *M. aeruginosa* Kütz. These species are listed in the order of their abundance. All are present in algal masses throughout the season, but *M. protocystis* increases enormously in numbers during August. The species is described by Crow (1923) as having irregular, often diffuse colonies, with the plants generally dissociated. In this Minnesota material the colonies are very diffuse and the plants widely scattered. The abundance of this alga and its diffuse state are especially interesting in view of Naumann's (1925) in-

vestigations on the form of the colony (*M. aeruginosa*) in relation to water movement. He concluded that large colonies, in part clathrate, with diffuent gelatine and scattered cells, develop in quiet water; while small, compact colonies develop in moving water. In the interior of these algal masses, where there is a minimum of water movement, the most common species is that having the maximum degree of dissociation.

**Coelomoron** gen nov. Tegumentum prope aut in totum invisibile, achromaticum, tenue, diffuente; coloniae microscopicae, globosae, ellipticae, aut ovatae, principio solidae, tum denique cavae; plantae coloniarum maturarum peripherice ordinatae in strato 2-3 cellularum; cellularum divisio primo in omnem directionem, tum denique tantum in angulis dextris ad superficiem coloniae.

Tegument almost or entirely invisible, colorless, thin, diffuent; colonies microscopic, spherical, elliptical, or ovoid, at first solid, later hollow; plants of mature colonies peripherally arranged in a layer of 2-3 cells; cell division at first in all directions, later only at right angles to the surface of the colony.

The genus differs from *Microcystis* in that a hollow colony is formed at maturity, and from *Coelosphaerium* in that the plants are arranged in a layer 2-3 cells thick, instead of in a single layer.

**Coelomoron regularis** spec. nov. (figs. 2 & 3). Tegumento prope aut in totum invisibili, achromatico, tenui, diffuente; coloniis microscopis, globosis, ellipticis, aut ovatis; coloniis immaturis usque ad  $30\mu$  crassis, solidis; coloniis

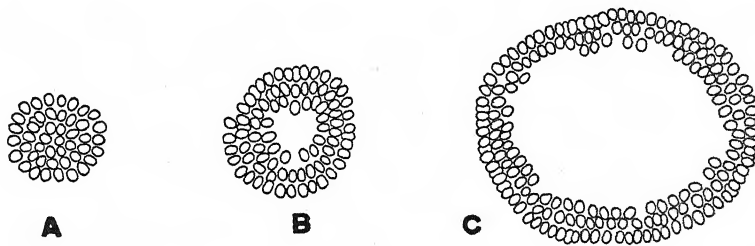


Fig. 3. *Coelomoron regularis* H. F. Buell spec. nov. Optical cross sections. A. Young colony. B. Older colony. C. Mature colony. Camera lucida drawings.  $\times 375$ .

maturis cavis; plantis confertis compositis, peripherice ordinatis in strato 2-3 cellularum, globosis aut ovatis, saepe leviter planis propter mutuam pressuram praesertim in faciebus in angulis dextris ad superficiem coloniae; protoplasmate laete aeruginoso, sine pseudoracuolis. Tegumento 2-4 $\mu$  crasso extrinsecus plantam. Coloniis usque ad  $250\mu$ , plerumque minus quam  $100\mu$ . Plantis 3-5 $\mu$  diametro.

Tegument almost or entirely invisible, colorless, thin, diffuent; colonies microscopic, spherical, elliptical, or ovoid; immature colonies up to  $30\mu$  in

diameter, solid; mature colonies hollow; plants crowded, peripherally arranged in a layer of 2-3 cells, spherical or ovoid, often slightly flattened because of mutual pressure especially on the faces at right angles to the surface of the colony; protoplasm bright blue-green, without pseudo-vacuoles. Tegument 2-4 $\mu$  thick outside of the plants. Colonies up to 250  $\mu$ , usually less than 100  $\mu$  in diameter. Plants 3-5 $\mu$  in diameter.

Type locality: Mud in interior of algal mass, 10-20 feet of water, Lake of the Isles Lagoon, Minneapolis, Minn.

This alga is found occasionally as a rare to common constituent of the interior portion of the community. The colonies are remarkable for their "neat" compactness, and for the regular arrangement of the plants (Fig. 2), unlike anything found in *Microcystis*. The optical cross sections (Fig. 3) show the angularity of the cells, as well as successive stages in the formation of the interior cavity of the colony. The interior of the colony sometimes appears quite transparent and homogeneous; more often fine granulations are present, probably bacterial in nature.

*Coelosphaerium Nägelianum* Ung. is present in the interior of the community rarely or commonly. The development of the species is favored by the same conditions as favor the development of pseudo-vacuolate species of *Microcystis*.

*Merismopedia* species present in the interior core include *M. convoluta* Bréb., which is present rarely or commonly in practically all masses, *M. elegans* A. Braun and *M. glauca* (Ehrenb.) Näg., which are occasionally present, and *M. punctata* Meyen, which is rare to very abundant.

*Merismopedia punctata*<sup>1</sup> (fig. 4) is of special interest. It is one of those species (see Geitler, 1932) in which the long axes of the cells are parallel with the plane of the colony, instead of being at right angles to it. The diameter of the cells which is at right angles to the surface of the colony is approximately the same as the shorter diameter seen in surface view—about 2 $\mu$  (fig. 4 E). This means that the plants are attached to each other by a very small area, as compared with the condition in such species as *M. convoluta*. Hence the plants break apart readily and the colonies

<sup>1</sup> As far as I have found, all references to this plant, beginning with Kützing (1849, p. 472), which state the place of publication, give it as Wiegmann's Archiv für Naturgeschichte 5: 67, 1839. Earlier, however, Meyen (1829, pl. 43, fig. 36) had figured the plant but did not name it. In 1839 in his *Pflanzen-Physiologie* (pp. 440-441) he named and described the plant. During the same year in Wiegmann's Archiv für Naturgeschichte he referred to his naming and description of 1839, in his physiology, as having occurred prior to his brief comment in the Archiv. Hence, *Pflanzen-Physiologie* 3: 440, 1839 is the original place of publication of the species *Merismopedia punctata* Meyen.

never attain any great size. Colonies having as many as 128 plants are rare; 32 is the usual maximum.

In the Minnesota material the cells are much more variable in size than as given by most authors—i.e.,  $2.5\text{--}3.5\mu$  in diameter. The maximum range, including all stages of growth (see below), is  $.8\text{--}2.6 \times 1.2\text{--}3.9\mu$ . Even in the normal blue-green phase (fig. 4 A-D), the cells range in their greatest diameter from  $1.8$  to  $3.9\mu$ .

For the most part division and growth appear to be practically simultaneous in all plants of a colony, resulting in individuals of approximately

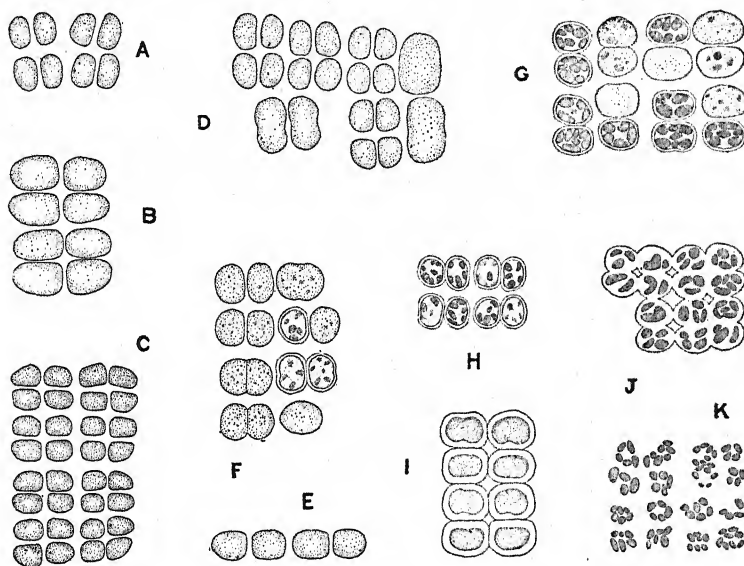


Fig. 4. *Merismopedia punctata* Meyen. A-D. Colonies showing arrangement and size of cells. E. Edge view of colony. F-K. Stages in vacuolation of colonies.  $\times 2000$ .

the same size (fig. 4 A-C). Irregularities in size sometimes occur where "division rhythm" is lacking. In a few collections many colonies are found in which this rhythm is absent, and those cells in which the impulse toward division is absent continue to increase in bulk practically in unison with other pairs or groups of cells (fig. 4 D). Except for such comparatively rare instances, the colonies of this species show remarkably regular cell arrangement.

In normal vegetative condition the protoplasts are gray to pale blue-green, as Smith (1920) states. However, under some conditions the color and appearance change. Viewed under low and high powers of the microscope, each cell appears as a bright, rose-violet vacuole surrounded by a



hyaline blue sheath (fig. 4 I). Under oil immersion (fig. 4 H), however, the vacuolate portion appears to consist of large, bright, dark rose bodies (Klincksieck and Valette, 1908, colors 6-7, 27-28), imbedded in a straw-colored matrix (colors 103, 128). The exterior portion seems narrower than under high power, but retains its hyaline, blue, cartilaginous appearance. Frequently in one colony (fig. 4 F, G) there may be found stages in the development of the vacuolate condition from the normal bluish-green cells, showing conclusively that the former is but a phase of the latter. The homogeneously granular cell contents become coarsely granular; the background becomes faintly straw-colored; and the granules seem to aggregate in small groups, at first indistinct in outline. The exterior portion appears gradually, at first wider than later, and indistinctly limited within. Eventually all the cells in a colony become vacuolated (fig. 4 H). When conditions are such that these vacuolations form, the growth of the cells is decreased, but division continues. In consequence, the average size of these rose-colored cells is smaller than that of the blue-green cells, about  $1.5 \times 2\mu$ , as compared with  $1.9 \times 2.5\mu$ . Later the outline of the plants disappears, except around the outside of the colony (fig. 4 J), and still later this also disappears, and the colony consists merely of groups of rose-colored granules (fig. 4 K).

The nature and cause of the vacuolation of these cells is doubtful. The color, while resembling that found in blue-green algae supposed to possess phycoerythrin, has less purple in it, and the normal vegetative cells have none of the gray-violet tint characteristic of these algae, nor is there ever any evidence of pigment diffusing into the surrounding water. Neither have the vacuolations the familiar appearance characteristic of the pseudo-vacuoles found in such planktonic forms as *Microcystis flos-aquae*; and, in addition, while masses of the latter species appear pale yellow-green or cream-color, masses of *Merismopedia punctata* are bright rose-purple. There seems to be no doubt, however, that these vacuolations, like the pseudo-vacuoles of *Microcystis* (Van Goor, 1925) contribute to the buoyancy of the colony, as in mounts of the material the blue-green colonies sink to the slide, while the vacuolate colonies float at the upper surface of the medium. And, although the appearance of the plants is quite unlike that of pseudo-vacuolate planktonic algae, it seems probable that the vacuoles are physiologically similar, since they respond similarly to treatment with acid (Van Goor, *op. cit.*). By treating material of *M. punctata* with acid (a few drops of HCl or acetic acid added at the edge of the cover glass), the vacuolations are made to disappear, and cells such as those shown in figure 4 H assume the color and appearance of the blue-green stage; at the same time the colonies sink and rest on the slide.



That the vacuolation of these algae is a stage in the process of disintegration seems likely. This conclusion is reached in view of the retarding or cessation of growth in vacuolate colonies, the ultimate breaking up of the plants into separate granules, and the fact that in the laboratory they form a flocculent purple scum on the surface of material which has been standing some days in a warm room and which is well advanced in disintegration. The conditions causing vacuolation are peculiar to the individual community, since on the same day one collection may show chiefly non-vacuolate and another chiefly vacuolate colonies of *M. punctata*.

With regard to the position of *M. punctata* within the genus, it should be noted that there is a sharp distinction between this species and *M. convoluta* in respect to the direction of elongation of the cells. If we accept as valid Troitzkaia's (1922) separation of *Coccopedia* from *Holopedia* on the basis of the former having round cells, while the latter has cells elongated at right angles to the plane of the colony, then it would seem equally proper to separate into a new genus *M. punctata* and related species which have the long axes of the cells parallel with the plane of the colony. On the other hand, in view of the gradations that exist between the genera of the plate-forming Cyanophyceae (*Merismopedia*, *Coccopedia*, *Holopedia*), there is the opinion of Ryppowa (1925) to consider. He places these groups as subgenera of the single genus *Merismopedia*. It would thus seem reasonable to separate into a subgenus those members of the genus *Merismopedia* (as generally understood) which have their long axes parallel to the plane of the colony.

Next, the synonymy given by Geitler (1932) is to be considered. He says: "Inc. *M. paludosa* Bennet, Journ. R. Micr. Soc. P. 4, Taf. 1, Fig. 1, 1886?—*M. thermalis* Kützing, Tab. phyc. 5, Taf. 38.—*M. convoluta* f. *minor* Wille, Alg. Zentrales, Sven Hedin, 1922.—*M. glauca* var. *fontinalis* Hansg., Prodr. Alg. Fl. Böhmen, 2, S. 141, 1892."

After examination of Bennett's (1886) article, it appears to me impossible to include *M. paludosa* with *M. punctata*: the cells, according to Bennett, have a diameter of  $12.5\mu$ ; Bennett himself questioned whether or not the plant belonged to the genus *Merismopedia*; and his figure indicates that he probably had a species of *Tetrapedia*.

Kützing's (1849) *M. thermalis*, judging from its size and general description, may perhaps be synonymous with *M. punctata*.

It seems doubtful if *M. convoluta* f. *minor* Wille (1922) can be included with *M. punctata* as the size is incorrect. Wille says: "Long. cell  $4-5\mu$ , lat.  $2-3\mu$ ." Even in the abnormally large cells in which division has failed to occur (see above) the largest size of *M. punctata* found in my material

is  $3.9\mu$ . Wille's figure represents plants which strongly resemble *M. convoluta*.

Whether or not *M. glauca* var. *fontinalis* Hansgirg (1892) should be included with *M. punctata* it is difficult to determine from the description.

The following paragraphs take up the question of synonymy as it appears to me.

In its vacuolate stage *M. punctata* agrees well with Wittrock's (1889) description of *M. chondroidea* Wittr. in the matter of color, granulation, wall characters, size of cells, and character of the colony.<sup>2</sup> Geitler (1925) separates *M. chondroidea* from *M. punctata* on the basis of the presence of vacuoles in *M. chondroidea*, although he says that it probably does not belong to the genus *Merismopedia*. Geitler (1932) says that *M. chondroidea* is an aberrant form which is best removed from the genus.

A specimen from Wittrock's material<sup>3</sup> has been examined and compared with the Minnesota material. Most of Wittrock's material consists of blue-green cells which appear to be typical *M. punctata*. Only a few colonies are present in which some or all of the cells are vacuolate. These, however, appear to be quite typical of the vacuolate phases found in the Minnesota collections of *M. punctata*. In the latter material vacuolate cells, when soaked up after having been dried, usually are blue-green in color, only occasional cells retaining their vacuolations and rose color. In view of these facts, I am convinced that the alga which Wittrock named *Merismopedia chondroidea* is a phase of *M. punctata* Meyen.

Closely similar to *M. punctata* is another species of *Merismopedia*—*M. tenuissima* Lemm. Lemmermann (1898) described it as having cells  $1.3\text{--}2\mu$  in size, pale blue-green, closely compressed into families of 16 cells. Smith (1920) and Geitler (1932) state that the number of cells in a colony is 16 to 100. Geitler separates this species from *M. punctata* on the basis of cell size, *M. tenuissima* having cells  $1.3\text{--}2\mu$  in diameter, while *M. punctata* has cells  $2.5\text{--}3.5\mu$  in diameter. Nevertheless, in the Minnesota material the range of cell sizes— $1.2\text{--}3.9\mu$ —includes the sizes given by Geitler for both *M. punctata* and *M. tenuissima*. Smith (1920) distinguishes between these two species on the basis of the distance between cells, *M. tenuissima* having the cells closely compressed and *M. punctata* having the cells "some distance from one another." His figures agree with this

<sup>2</sup> "M. cellulis cytoplasmate purpurascens-violaceo, granulis, sulphuraceis nullis, membrana crassa quasi chondroidea; diametro cellularum sphaearum 2, 4-2,  $6\mu$ ; coenobii 4 vel 8-(rarius 2, 12, 16) cellularibus, in glomerulos saturate violaceos, forma indefinita, in superficie aquae demum natantes coacervatos."

<sup>3</sup> Wittrock and Nordstedt, no. 200, kindly supplied by the late Dr. M. A. Howe of the New York Botanical Garden.

statement. In a later publication, however, Smith (1924) figures a colony of *M. tenuissima* having cells farther apart than those shown in his 1920 figure of *M. punctata*. And Fritsch (1912) figures *M. tenuissima* with cells both close together and wide apart. In the Minnesota material some colonies are found which agree with Smith's (1920) figure of *M. tenuissima*, others which agree with his figure of *M. punctata*, and many which are intermediate. Hence, it appears probable that *M. tenuissima* and *M. punctata* are synonymous.

Lemmermann (1900) described another species, *M. Marssonii* Lemm., having many similarities with *M. tenuissima*, but distinguished from it by the presence of gas vacuoles, which, however, disappeared on treatment with acids. In view of what has been said with regard to the relation between the blue-green phase of *M. punctata* and its vacuolate stage, which has been described as *M. chondroidea*, there seems little doubt that Lemmermann's *M. Marssonii* is the vacuolate phase of his *M. tenuissima*. If this be true, it then seems that *M. Marssonii* Lemm. and *M. punctata* Meyen are synonymous.

Bachmann (1920) described still another vacuolate species, *M. Trolleri*. The plants formed a dull violet mass which was driven on to the beach by the wind. The colonies were 8-celled, sometimes 16-celled. The cells were 2-3 $\mu$  in diameter, each cell possessing a thick sheath. The contents consisted of wine-red granules, "die oft in die Hülle herausquellen." Except that the size of these plants is a trifle larger than the average size of the vacuolate plants of *M. punctata*, Bachmann's description and figures fit very well the vacuolate phase of *M. punctata*. The expression "Kügelchen, die oft in Hülle herausquellen" appears to be descriptive of such a stage as is pictured in this paper in figure 5 J, K, when disintegration of the plants is well advanced. While in the Minnesota material the algae do not as a rule occur in macroscopic masses, they do occasionally; in laboratory cultures quantities of *M. punctata* at times form a dirty violet scum at the water surface; and in the stagnant arm of a lake in western Wisconsin I have found the vacuolate phase of *M. punctata* producing just such masses as Bachmann describes. In view of these facts, it appears probable that *M. Trolleri* is the same as *M. punctata*.

*Holopedia geminata* Lagerh. is present in the interior of communities occasionally, sometimes common, especially when in company with *Merismopedia convoluta*.

***Holopedia pulchella* spec. nov. (fig. 5).** Coloniis minutis; plantis irregulariter dispositis, confertis compositis, polygonie planis; protoplasmate laete aeruginoso; plantis 2.5-4.8 $\mu$  diametro (facies coloniae), 3.4-5.3 $\mu$  longitudine (extremitas coloniae).

Colonies small; plants irregularly placed, closely compressed, polygonally flattened; protoplast bright blue-green; plants  $2.5\text{--}4.8\mu$  in diameter) surface of colony,)  $3.4\text{--}5.3\mu$  long (edge of colony).

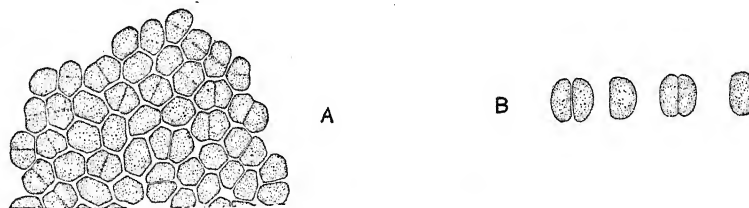


Fig. 5. *Holopedia pulchella* H. F. Buell spec. nov. A. Portion of surface of colony. B. Longitudinal views of cells.  $\times 1000$ .

Type locality: Mud in interior of Cyanophycean algal mass, 10–20 feet of water, Lake of the Isles Lagoon, Minneapolis, Minn.

Occurrence: *Holopedia pulchella* is rare, or occasionally common, in the interior portion of the community, usually in company with *H. geminata* and *Merismopedia convoluta*.

Remarks: *H. pulchella* differs from the most closely related species, *H. sabulicola* Lagerheim, in four particulars: 1) colonies unattached; 2) colonies living in fresh water; 3) plants crowded; 4) plants smaller.

Lagerheim (1883) found *H. sabulicola* in the Baltic Sea, attached to grains of sand along with species of *Merismopedia*. The Minnesota material has been compared with a fragment from Lagerheim's specimen.<sup>4</sup> The plants are similar in general appearance, except that in *H. pulchella* they are more crowded and angular, and are considerably smaller than in

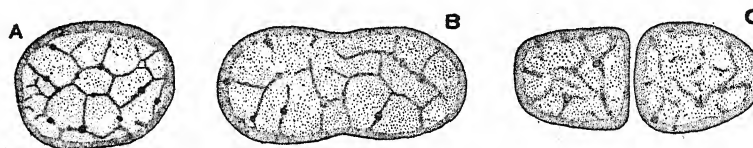


Fig. 6. *Synechococcus aeruginosus* Nägeli.  $\times 1000$ .

*H. sabulicola*. The latter is described by Lagerheim as having cells  $6\mu$  long, and in his dried material they have been found to be  $6\text{--}6.8\mu$  in length.

*Synechococcus aeruginosus* Nägeli (Fig. 6) is rare or common in the interior portion of most masses. The plants are from  $13$  to  $16\mu$  in diameter. The color is a pale greenish-gray, and the general appearance is like that

<sup>4</sup> Wittrock, Nordstedt, and Lagerheim no. 1549, kindly furnished by the late Dr. M. A. Howe.

shown by Geitler (1932). The pigments, however, instead of being peripheral, seem to be in the interior of the cell, where they are confined to anastomosing strands. At intervals in the pigmented strands the granular substance is aggregated into larger masses which stand out brightly from the rest of the cell substance. The pronounced differentiation of the protoplasm into pigmented and unpigmented areas, and particularly the interior pigmented strands, is distinctive. It is true that Chodat (1896) found a pigmented central network in *Chroococcus turgidus* (Kütz.) Näg., and Crow (1922) refers to Chodat's work and also speaks of "shining globules of pigment within the cell" of some species of *Chroococcus*. While their words might seem to be in some measure descriptive of *Synechococcus aeruginosus*, nevertheless, as far as I have observed, and as far as available figures indicate, the appearance of the protoplast of *Chroococcus turgidus* is quite unlike that of *Synechococcus aeruginosus*. Indeed the distribution of pigments in the latter plant is much more suggestive of that in the red alga *Porphyridium* (Geitler, 1924) with its stellate, central chromatophore with strands reaching out to the periphery of the cell.

#### OSCILLATORIACEAE

*Spirulina aeruginea* spec. nov. (Section *Arthrospira* Geitler) (fig. 7). Strato viride-nigro; trichomatibus in spiras laxas regulares, vertes ab latere dextro ad latus sinistrum, apicibus gradatim attenuatis, ad dissepimenta haud constrictis; dissepimentis plerumque distinctis, interdum granulatis; cellulis diametro brevioribus cellula apicali plerumque diametro longiore; protoplasmate tenui-granuloso, ad dissepimenta crasse granulato, laete aeruginoso; spiris 9.5–18 $\mu$  crassis, 14–24 $\mu$  inter versationes; cellulis 3.9–5.7  $\times$  3.5–5 $\mu$ .

Plant mass greenish black; trichomes in loose regular spirals, turning from right to left,<sup>5</sup> gradually tapered at the apex, not constricted at the transverse

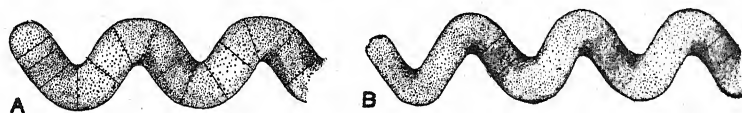


Fig. 7. *Spirulina aeruginea* H. F. Buell spec. nov.  $\times 1000$ .

septa; transverse septa usually distinct, sometimes granulated; cells shorter than their diameter; apical cell usually longer than the diameter; protoplasm finely granular, at the transverse septa sometimes coarsely granulated, bright

<sup>5</sup> In speaking of the direction of the spiral, the reference is to the direction as seen under the microscope, where of course the apparent direction is the reverse of the actual.



blue-green;<sup>6</sup> spirals  $9.5\text{--}18\mu$  broad,  $14\text{--}24\mu$  between turnings; cells  $3.9\text{--}5.7 \times 3.5\text{--}5\mu$ .

Type locality: Outer layers of Cyanophycean algal mass, 10–20 feet of water, Lake of the Isles Lagoon, Minneapolis, Minn.

Occurrence: *Spirulina aeruginea* is one of the characteristic and distinctive members of the community. With its allied species, *S. amethystina* H. F. Buell, and species of *Oscillatoria*, it forms the outer layers of the mass. During the summers of 1929 and 1930, *S. aeruginea* was more abundant than *S. amethystina* until the latter part of the season. Throughout the season of 1931, when beginning early in the summer the temperatures were unusually high, *S. aeruginea* was much less abundant than *S. amethystina*.

Remarks: *Spirulina aeruginea* is distinguished from *S. Jenneri* (Hassall) Kützing<sup>7</sup> in three particulars: 1) the diameter of the trichome— $3.9\text{--}5.7\mu$ —is somewhat less than in *S. Jenneri*, whose diameter is given as  $5\text{--}8\mu$ ; 2) the extremity of the trichome tapers, while the trichome of *S. Jenneri* is untapered; 3) the spiral has a clockwise direction, while in *S. Jenneri* it has a counter-clockwise direction.

With regard to the direction of spiraling in the genus *Spirulina*, there is little information in the literature. Many of the earlier published figures do not indicate a spiral. No authors, as far as I know, state whether or not they consider the direction of spiraling constant in the species they describe. Geitler (1925) says that the direction of spiraling should be used as a diagnostic character, indicating that he considers it constant. In most of the published figures of *S. Jenneri*, including the widely copied drawing by Gomont (1892), the plant is drawn as if the entire body of the trichome lay in a single plane. As far as I have been able to discover, the only delineators who have indicated the direction of the spiral are Hassall (1845), Wolle (1887), Crow (1924), Frémy (1930) and Moore.<sup>8</sup> All of these

<sup>6</sup> Klincksieck and Valette (1908) colors 336, 342.

<sup>7</sup> The specific name of this plant is variously credited—rarely to Hassall, generally either to Kützing or to Stizenberger. The first use of the name, however, appears to have been by Hassall (1845) in *Spirillum Jenneri*. Kützing (1846, 1849) used the name *Spirulina Jenneri* Kützing. Stizenberger (1852) placed Hassall's plant in his new genus *Arthrospira*. Gomont (1892), the universally accepted authority on the Oscillatoriaceae, gives the name *Arthrospira Jenneri* Stizenberger, but in his list of synonyms gives *Spirillum Jenneri* Hassall and *Spirulina Jenneri* Kützing. Hence if the genus *Arthrospira* is retained, the name of the species is *Arthrospira Jenneri* (Hassall) Stizenberger; while if it is returned to the genus *Spirulina*, the name is *Spirulina Jenneri* (Hassall) Kützing.

<sup>8</sup> Moore, Marjorie Forbes—Department of Botany, University of Minnesota, unpublished observations.



indicate a counter-clockwise, or left to right, spiral. Likewise I have found in collections of bottom sand from the littoral region (10–20 cm.) in Lake of the Isles Lagoon typical *S. Jenneri* having counter-clockwise spirals. Consequently there is little doubt that a counter-clockwise direction of spiraling is characteristic of *S. Jenneri*. A clockwise direction of spiraling is definitely characteristic of *S. aeruginea*.

***Spirulina amethystina* spec. nov.** (Section *Arthrospira* Geitler) (fig. 8). Strato levi nigro aut rubro; trichomatibus in spiras laxas regulares, vertes ab latere dextro ad latus sinistram, apicibus gradatim attenuatis, ad dissepimenta haud constrictis; dissepimentis plerumque distinctis, interdum granulatis; cellulis diametro brevioribus; cellula apicali plerumque diametro longiore; protoplasmate tenui-granuloso, ad dissepimenta interdum crasse granulato, viride-cinereo aut violaceo; spiris  $9.5\text{--}18\mu$  crassis,  $14\text{--}24\mu$  interversiones; cellulis  $3.9\text{--}5.7 \times 3.5\text{--}5\mu$ .

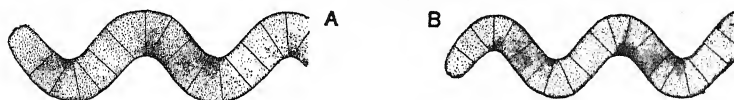


Fig. 8. *Spirulina amethystina* H. F. Buell spec. nov.  $\times 1000$ .

Plant mass soft black or red; trichomes in loose regular spirals, turning from right to left,<sup>9</sup> gradually tapered at the apex, not constricted at the transverse septa; transverse septa usually distinct, sometimes granulated; cells shorter than their diameter; apical cell usually longer than the diameter; protoplasm finely granular, at the transverse septa sometimes coarsely granulated, grayish green to violet;<sup>10</sup> spirals  $9.5\text{--}18\mu$  broad,  $14\text{--}24\mu$  between turnings, cells  $3.9\text{--}5.7 \times 3.5\text{--}5\mu$ .

Type locality: Outer layers of Cyanophycean algal mass, 10–20 feet of water, Lake of the Isles Lagoon, Minneapolis, Minn.

Occurrence: *Spirulina amethystina* is one of the dominant members of the association which forms the outer layer of the mass. It is most abundant during extremely hot weather.

Remarks: This species is distinguished from *S. aeruginea* by its gray to violet color, instead of a typical blue-green color. While in the grayer phase of pigmentation of *S. amethystina* the purple tint is not noticeable, and while there are indistinguishable gradations from green-gray to distinct purple or violet, nevertheless there is no gradation in color between the green-gray of *S. amethystina* and the bright blue-green of *S. aeruginea*.

<sup>9</sup> In speaking of the direction of the spiral, the reference is to the direction as seen under the microscope.

<sup>10</sup> Klincksieck and Valette (1908) colors 498, 517, 522, 533, 538, 548, 572.

The difference in color is striking in cases where trichomes of the two species twine about one another. It is probable that the purple color of *S. amethystina* is due to the presence of phycoerythrin, and that this pigment is entirely lacking in *S. aeruginea*. In view of this probability, and in view of the increasing tendency (Tilden, 1928) to consider pigmentation in the algae as a fundamental, elemental character of the organism, it seems desirable to consider *S. amethystina* as a distinct species.

With regard to the pigmentation of *S. amethystina*, one feature is of interest in connection with the theory advanced by Crow (1922, 1928) that the trichome of the Oscillatoriaceae is homologous with the single cell of the Chroococcaceae. While there is a wide variation in color from trichome to trichome, the color is constant within the individual trichome throughout its entire length, however great. There are also other indications that the trichome is the unit of structure in both *S. amethystina* and *S. aeruginea*; there is practical uniformity throughout the trichome in the degree of granulation of the protoplasm in both living and preserved plants; and there is considerable uniformity in the visibility of the transverse septa.

One point should be mentioned, however, which Crow (1928) makes in support of his theory of the homology between trichomes and unicellular plants. Of the genus *Arthrospira* he says: "The plants retain their hormogonial aspect throughout their life. The filaments of *Arthrospira* are, like those of *Spirulina*, amongst the shortest adult forms occurring in the family Oscillatoriaceae." Nevertheless, in *S. amethystina* and *S. aeruginea* the trichomes are fully as long as are those of accompanying species of *Oscillatoria* having a similar diameter. In any case, trichomes attaining a length of 1-2 mm., as are common in these two species of *Spirulina*, can hardly be said to have a "hormogonial aspect."

Species of *Oscillatoria* present in the exterior layers of the community are *O. geminata* Menegh., *O. amphibia* Agardh, *O. limosa* Agardh, *O. Mougeotii* Kütz., *O. tenuis* Agardh, *O. princeps* Vaucher, forma *maxima* (Kütz.) Rabenh. and forma *tenuior* Rabenh., *O. terebriformis* Agardh, *O. formosa* Bory, *O. Okeni* Agardh, and *O. chalybea* Mertens. All of these, except the last, are present in variable numbers, being rare to common. *O. chalybea*, however, is always present in considerable amount, and in masses which are blue-green or blackish-green in color, it is generally the dominant species in the outer layers. In addition there are present the following forms which are believed to be new to science.

***Oscillatoria amethystina*. spec. nov. (fig. 9).** Strato levi nigro aut rubro; trichomatibus rectis, flexilibus, ad dissepimenta plus minusve constrictis, gradatim attenuatis ad longinquitatem ab apiculo; apiculo uncinato aut arcu-

ato; cellula apicali obtuso haud capitata, haud calyptrata; cellulis subquadratis vel brevioribus; cellula apicali plerumque diametro longiore; protoplasmate tenui-granuloso, ad dissepimenta plus minusve crasse granulato, viride-cinereo aut violaceo; cellulis  $3.5-5 \times 2-3.5 \mu$ .

Plant mass soft black to red; trichomes straight, flexuous, more or less constricted at the transverse septa, gradually tapering for a long distance from the apex; apex hooked or curved; apical cell rounded, not capitate, not calyptrate; cells subquadrate or shorter; apical cell usually longer than the diameter; protoplast finely granular, more or less coarsely granulated at the transverse septa, greenish-gray to violet;<sup>11</sup> cells  $3.5-5 \times 2-3.5 \mu$ .

Type locality: Outer layers of Cyanophycean algal mass, 10-20 feet of water, Lake of the Isles Lagoon, Minneapolis, Minn.



Fig. 9. *Oscillatoria amethystina* H. F. Buell spec. nov. A. Terminal and median portions of a trichome. B. Portion of old, disintegrating trichome.  $\times 1000$ .

Occurrence: *O. amethystina* is rare or common in the exterior portions of masses throughout the season, but is most abundant during the hottest weather.

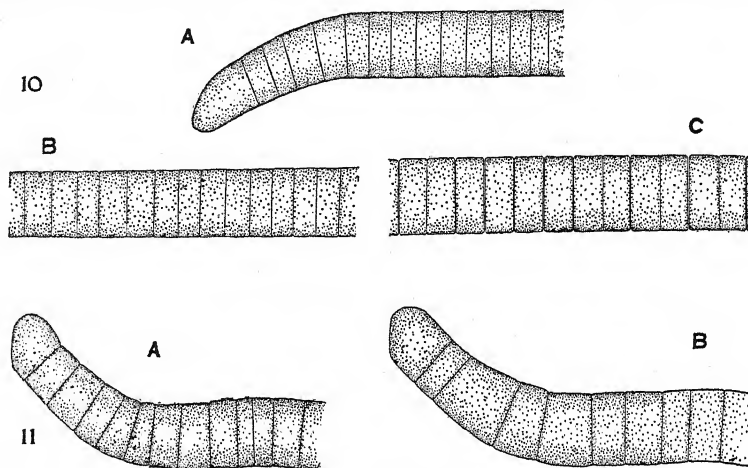
Remarks: This species appears to resemble most closely *O. violacea* (Wallr.) Hass., which has violet to blue-green trichomes,  $4-4.5 \mu$  in diameter. However, *O. violacea* is described as being sharply pointed at the apex, while *O. amethystina* does not taper to a sharp point, but is rounded at the apex. The appearance of the apical cell itself is much like that of the apical cell of *O. formosa* Bory, but in *O. amethystina* the tapering is greater and much more gradual. The trichome is usually much less constricted in the apical than in the median portion (fig. 9 A). The color of the plant is like that of *Spirulina amethystina*.

*Oscillatoria Leavittae*<sup>12</sup> spec. nov. (figs. 10, 11). Strato levi nigro aut rubro; trichomatibus rectis, ad dissepimenta plus minusve constrictis, gradatim attenuatis ad longinquitatem ab apiculo; apiculo uncinato aut arcuato; cellula apicali conica, plerumque leviter plana a parte superiore lateris convexi, haud capitata, haud calyptrata; cellulis diametro brevioribus, cellula apicali plerumque diametro longiore; protoplasmate tenui-granuloso, viride-cinereo aut violaceo; cellulis  $7.5-11.5 \times 3-7 \mu$ ; cellulis apicalibus usque ad  $11 \mu$  longis.

<sup>11</sup> Klincksieck and Valette (1908) colors 498, 517, 522, 533, 538, 548, 572.

<sup>12</sup> This handsome species is named in honor of Miss Clara K. Leavitt, who discovered and first studied the community in which the plant grows.

Plant mass soft black or red; trichomes straight, more or less constricted at the transverse septa, gradually tapering for a long distance from the apex; apex hooked or curved; apical cell conical, usually flattened on the upper portion of the convex side, not capitate, not calyptrate; protoplast finely granular, greenish-gray to violet;<sup>13</sup> cells  $7.5-11.5 \times 3-7 \mu$ ; apical cell up to  $11 \mu$  long.



Figs. 10-11. Fig. 10. *Oscillatoria Leavittae* H. F. Buell spec. nov. A, B, C. Terminal, subterminal, and median portions respectively of one trichome.  $\times 1000$ . Fig. 11. *Oscillatoria Leavittae* H. F. Buell spec. nov. Variations in apices of trichomes.  $\times 1000$ .

Type locality: Outer layers of Cyanophycean algal mass, 10-20 feet of water, Lake of the Isles Lagoon, Minneapolis, Minn.

Occurrence: *O. Leavittae* is the dominant species in the exterior portion of reddish black or red masses. It is most abundant during the hottest weather of the summer.

Remarks: In the size of the trichomes *O. Leavittae* is similar to *O. chalybea*, whose trichomes are  $8-13 \mu$  in diameter. The gradual tapering characteristic of the new species also is similar to the condition usually described for *O. chalybea*. The latter species,<sup>14</sup> however, is described as having an obtuse apical cell, while *O. Leavittae* is characterized by a conical apical cell, peculiarly flattened on the upper portion of the convex side. Also the color is distinctive, there being as great a difference between the color of *O. Leavittae* and *O. chalybea* as there is between that of *Spirulina amethystina* and *S. aeruginea* (see above). The color is like that of *Spirulina amethystina* and *Oscillatoria amethystina*, and as in these two species, the color is most pronounced in the hottest weather.

<sup>13</sup> Klincksieck and Valette (1908) colors 498, 517, 522, 533, 538, 548, 572.

<sup>14</sup> Gomont (1892) says, "apicem versus breviter aut longe et sensim attenuata"; Frémy (1930) says, "longuement et insensiblement atténués vers leurs extrémités." Both authors, however, figure a brief tapering.

The characters of the apical portion of the trichome are, of course, more or less variable, apparently depending on the amount of growth since breakage or formation of hormogones has occurred. Thus if a trichome has been recently broken, considerable growth must take place before the new apex becomes gradually tapered. Hence, for a time the apical cell will be more or less obtuse; but it soon acquires the characteristic flattening on the upper side of the curve (fig. 11).

In this plant, as in *O. chalybea*, there is usually a decided difference in long trichomes between the median and apical portions. The trichome is not merely wider in its median portion, it is also more strongly constricted (fig. 10 A, B, C), the protoplast is more coarsely granular, and the color is generally more pronounced. Apparently younger, actively growing portions of the trichome are greenish-gray, the red pigment being more abundant, or at least more evident, in older cells. The lack of uniformity shown by *Oscillatoria amethystina*, *O. Leavittae*, and *O. chalybea* as to constrictions, granulations and coloring of individual trichomes is in striking contrast with the condition shown by *Spirulina aeruginea* and *S. amethystina* (see above).

Species of *Anabaena* are present occasionally in the interior mud of the community. These include the pseudo-vacuolate species *A. planctonica* Brunnth, and *A. spiroides* Kleb., and two others, which in the absence of gonidia can not be identified.

Also *Anabaena constricta* (Szafer) Geitler (fig. 12) is present in prac-

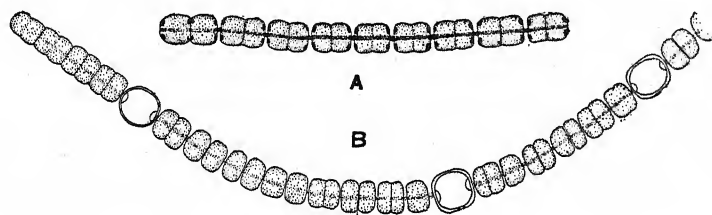


Fig. 12. *Anabaena constricta* (Szafer) Geitler. A. Filament without heterocysts. B. Filament with heterocysts.  $\times 1000$ .

tically all communities, sometimes commonly. The vegetative cells are  $5-7 \times 6-10 \mu$ . The colorless central portion of the filament has the appearance of a thread with beads strung on it. This "thread" is continuous from cell to cell, but it is very fragile and breaks readily; hence one rarely finds filaments composed of more than 15 or 20 cells. Geitler (1932) states that only two heterocysts (in one filament) have thus far been found (Koppe, 1924). Examination of hundreds of filaments in this material has disclosed one filament with three heterocysts (fig. 12 B). These



have a diameter of  $5-6\mu$  and a length of  $6-6.5\mu$ . Koppe reported a diameter of  $5\mu$ .

#### SUMMARY

A description is given of the blue-green algae forming a freshwater community which develops in bottom ooze and later floats to the surface. One new genus is described—*Coelomoron*—a colonial member of the Chroococcaceae. New species described are *Coelomoron regularis*, *Holopedia pulchella*, *Spirulina aeruginea*, *S. amethystina*, *Oscillatoria amethystina*, and *O. Leavittae*, the last three of which are characterized in part by red pigmentation. *Merismopedia chondroidea* Wittr. is shown to be synonymous with *M. punctata* Meyen.

This work was done in the botanical laboratories of the University of Minnesota.

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RALEIGH, N. C.

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## The Cactaceae of Southern Utah

ELZADA U. CLOVER  
(WITH PLATES 15-19)

A field survey of the Cactaceae in a part of southern Utah yielded interesting material and new information regarding distribution of cacti. The work was sponsored by Mr. E. J. Marston of Colorado Springs, Colorado, who is interested in furthering a systematic and phytogeographic study of the family.

The author was accompanied and assisted by Miss Carol Davidson of Colorado Springs; and although the time (July 31 to August 15) was brief in which to cover so much territory, the results were gratifying. Many of the roads in the following counties were traversed: Grand, San Juan, Kane, Washington, Iron, Garfield, Wayne, and Emory.

This territory is drained chiefly by the Green and Colorado Rivers and their tributaries. The Virgin River has its origin in western Kane County and flows through Washington County. Most of southern Utah belongs to the Plateau province as defined by Powell. The extreme southwestern portion is included in the Great Basin.

This part of Utah holds a special interest for the botanist because it is within the northern limits of the Lower Sonoran desert zone, although theoretically most of it should be northern desert. The flora has not been well studied because of the scarcity of population and lack of roads. Thousands of square miles of southeastern Utah are entirely unsettled and a pack train with a competent guide who knew the country well enough to find waterholes would be necessary for thorough exploration.

Clay and sandstone of the Jurassic and Triassic cover the major part of counties studied. The exposed rocks range from whitish-pink to deep red sandstone, and light to chocolate shales with outcrops of limestone.

The cacti extend their ranges more slowly than many plants, because they grow slowly and have no special modifications insuring seed dissemination. Without question, the ranges of many species have been limited by physiographic features; some cacti are found on one side of a mountain range and not on the other, although conditions appear to be practically the same on both sides. Where such barriers exist, distribution follows water courses. The canyons and cuts in the vicinity of Fruita have a more southern flora than one would expect, since the upland here belongs to the piñon zone. The lower altitude may have some influence, but it is thought that the Lower Sonoran flora follows the valleys since migration over the high plateaus is impossible.

Altitude has a decided effect on vegetation, the lowlands having a growing season two to three times as long as that of the high plateaus. The precipitation in general is greater at higher altitudes, although St. George with an altitude of only 2880 feet has a greater rainfall than Loa with an altitude of 7000 feet. Navajo Mountain, judging by the vegetation, receives an annual rainfall exceeding 20 inches; while the surrounding country has a very meager rainfall, and little or no vegetation in places as a result.

Soil seems to be more of a limiting factor for some species than others. *Echinomastus Johnsonii* apparently needs calcareous soil. The *Echinocerei* also can be found on limestone ledges or on sand mixed with limestone without so much regard to altitude or moisture, but the caespitose form of *Pediocactus* and the western *Coryphanthae* are confined to the higher altitudes and show greater latitude in the matter of soil tolerance. The solitary form of *Pediocactus* grows at a lower altitude than the other but is found at its best under rather moist conditions, often close to streams or standing water. Several species of cacti in the vicinity of St. George have either abruptly reached the northern limit of their range or are limited by other factors than climatic. The lower altitude and correspondingly higher temperature in the extreme southwestern part of the state may account for the richness of the sub-tropical cactus flora.

It is possible that soil conditions may be at least partially responsible for northern limits of range. The Precambrian strata are exposed in this section and extend over the portions of Nevada, California and Arizona occupied by these same species. They are characterized by limestones which may have the same distribution as the characteristic plants of the region.

Catastrophes have played some part in retarding distribution. *Opuntia polyacantha* and *Sclerocactus Whipplei* can be found in fair abundance, north of Bluff, but the plants are mostly dead or dying probably from drought. An annual rainfall of three inches has been reported for Bluff. Farther east in the dust bowl region skeletons of numerous plants testify to the effect of changing conditions there. Flood waters in mountainous areas destroy species which may be migrating, and may on the contrary deposit plants or seeds which become established in a new territory.

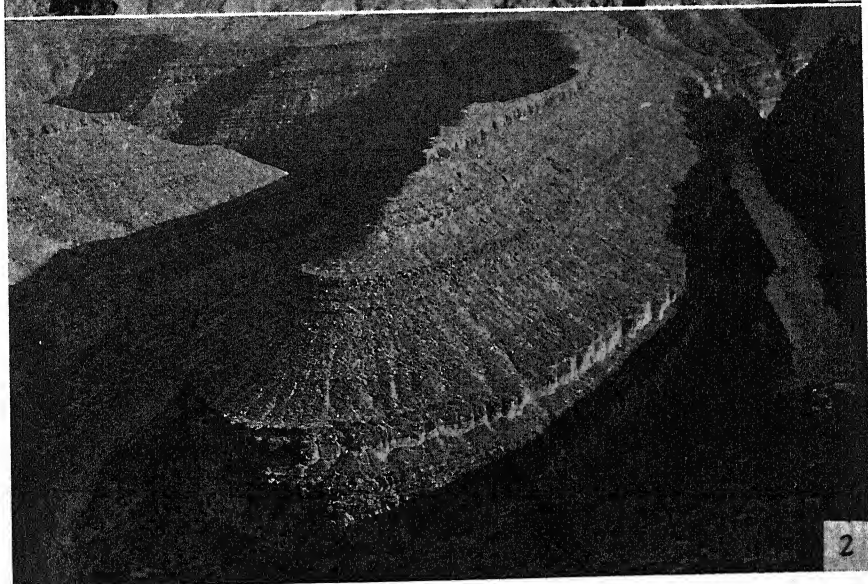
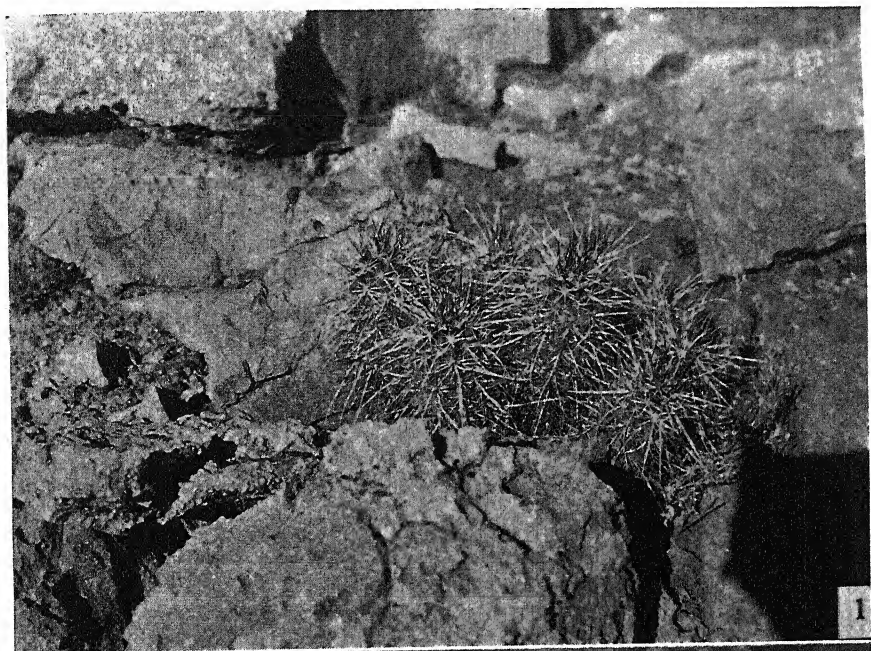
It is interesting to note the variation within a species throughout a

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#### Explanation of Plate 15

Fig. 1. *Echinocereus Engelmannii* reported to have white flowers. Growing on limestone near the San Juan River (fig. 2).

Fig. 2. The "Goosenecks," cut through shale and sandstone by the San Juan River, Mexican Hat, San Juan Co., Utah.



CLOVER: CACTACEAE



range of fifty to several hundred miles, particularly in a north and south direction. The change in form and character is often so gradual that it can scarcely be detected, but plants from the extremes of these ranges can often scarcely be recognized as belonging to the same species. Specific examples are *Opuntia fragilis* and *Opuntia polyacantha*; *Echinocereus Reichenbachii* and some of the opuntias growing farther east also vary greatly.

The family is generally thought of as young from the evolutionary standpoint in such aggressive genera as *Opuntia*. There are, however, locally restricted types of no very obvious affinity that give the impression of being possibly ancient. Such a one is *Utahia Sileri*, which is very different from other cacti in the region and has a limited distribution. If this is the method of evolution, we are presented with the necessity of accounting for apparently continuous variation as the specific range is traversed, on the ground of successive cumulative changes in the same direction. Of course "place effect" may be of greater magnitude than seems likely. The seemingly continuous gradations afford magnificent material for genetic research bearing on the problem of climatic and habitat adaptation.

#### LIST OF SPECIES

*OPUNTIA RAMOSISSIMA* Engelm., Amer. Journ. Sci., Series 2, 14: 339. Specimens collected at Beaver Dam Wash, Washington Co. by a citizen of St. George (1870). This is an odd species of the subgenus *Cylindropuntia*, with no close relatives. Reported hitherto from southern Nevada, western Arizona, southeastern California and northwestern Sonora.  
HABITAT: Dry desert flats.

*OPUNTIA WHIPPLEI* Engelm. & Bigelow, Proc. Amer. Acad. 3: 307. 1856. Kanab, and Johnson, Kane Co. (1883); Enterprise, St. George, Washington Co.; Santa Clara Valley, Iron Co. Reported elsewhere from northern New Mexico, Arizona and southwestern Colorado.

HABITAT: Sandy calcareous soil on south and west slopes, also on sandy flats, associated with Joshua trees, *Ferocactus acanthodes*, *Echinomastus Johnsonii* and *Echinocereus Engelmannii* at St. George, Washington Co.; on red sandstone in Kane Co.; on rocky slopes near Enterprise, Washington Co.

*OPUNTIA ACANTHOCARPA* Engelm. & Bigelow, Proc. Amer. Acad. 3: 308. 1856. South of St. George, Washington Co. (1882). This species is probably most abundant in Arizona although it is found in California near the Nevada state line and the Colorado River; also common in Nevada.

HABITAT: Foothills or stony mesas, on limestone, sandstone and shale.

*OPUNTIA ECHINOCARPA* Engelm. & Bigelow, Proc. Amer. Acad. 3: 305. 1856. St. George, Washington Co. (1886); Kanab, Kane Co., Beaver Dam



Mts.; widespread in southern California and found in southern Nevada, northwestern Arizona and Sonora.

HABITAT: On mesas and slopes, limestone outcrops, sandstone and shale.

*OPUNTIA BIGELOVII* Engelm., Proc. Amer. Acad. 3: 307. 1856. South of St. George, Washington Co. (1890). This has previously been found in Nevada, Arizona, California, Lower California and Sonora.

HABITAT: In isolated colonies which are often miles apart; in sandy soil or in sand mixed with decomposed granite; in limestone outcrops usually on dry steep hillsides, south and west exposures.

*OPUNTIA BASILARIS* Engelm. & Bigelow, Proc. Amer. Acad. 3: 298. 1856. South of St. George in Joshua forest, Washington Co. (1887); Beaver Dam Mts.; present in northern Sonora, western Arizona, southern California and Nevada.

HABITAT: Calcareous soils on dry hillside; reported as growing also on river flood plains.

*OPUNTIA AUREA* Baxter, Journ. Cact. Succ. Soc. 5: (6). 1933. Between Kanab and Zion National Park, Kane Co. (1885) at an altitude of 6500 to 7000 ft.; reported also on both sides of the Arizona-Utah border near the Kaibab Indian Reservation; Cane Beds, Pipe Springs, between Zion Park and Carmel, Utah; west of the Kaibab Indian Reservation to the lower slope of the Sierras near Bishop, California. This is one of the Basilaes recently described, differing from *O. basiliaris* by having joints in a chain instead of in a truly basilar form.

HABITAT: South of Zion National Park on a dry, steep, clay hillside, associated with *Juniperus*.

*OPUNTIA BRACHYCLADA* Griffiths, Proc. Biol. Soc. of Washington, 27: 25, 1914. In the Dixie National Forest between Veyo and Enterprise, Washington Co. (1888). This species was not recognized by Britton and Rose but has been taken up by Baxter in his report on California cacti as a distinct species of the Basilaes. He collected the plant in Pine Canyon, Sheep Creek Canyon, Dead Man's Gulch, and Mescal Canyon all within fifteen miles. It has also been reported from above Big Bear Lake in the San Bernardino Mts.

HABITAT: West slope in sandy, calcareous soil. Only two clumps were found, but they were very characteristic.

*OPUNTIA PHAEACANTHA* Engelm., in Gray, Mem. Amer. Acad. 4: 52. 1849. LaSal, Grand Co.; Bluff, San Juan Co., Kanab, Kane Co. (1894), Gunlock, Washington Co., Torrey and Fruita, Wayne Co. This species is rather widespread, occurring in Arizona, California, New Mexico, Colorado, west Texas and northern Mexico.

HABITAT: Sandy plains, desert foothills and mesas, often associated with *O. polyacantha*.

*OPUNTIA RUBRIFOLIA* Engelm., ex Coulter, Contrib. Nat'l Herb. 3: 424,

1896. Between Comb Wash and Mexican Hat, San Juan Co. (1876). The type specimen was collected at St. George. The specimen collected at Mexican Hat is somewhat smaller than the type but apparently belongs here. New stems produced in the greenhouse have the characteristic red color.

HABITAT: Dark red sandstone and granite fragments. L. A. Woodbury (unpub.) reports a collection of this species in Zion National Park, Utah, April 23, 1930.

*OPUNTIA CHLOROTICA* Engelm. & Bigelow, Proc. Amer. Acad. 3: 291. 1856. Zion National Park, Washington Co., between Kanab and Johnson (1881), Kane Co. The distribution is Sonora and New Mexico to Nevada, Utah, Arizona, California and Lower California.

HABITAT: On rocky hillsides and mountains usually below 4200 feet.

*OPUNTIA FRAGILIS* (Nutt.) Haworth, Suppl. Pl. Succ. 82. 1819. Between Boulder and Torrey, Washington Co., Fruita, Wayne Co., Escalante, Washington Co., LaSal, Grand Co. (1873). This species has a wide geographic range and varies greatly in form under different conditions. It occurs in the Middle West from Wisconsin to central Kansas, and from northwest Texas to Arizona, Utah, Colorado, Oregon, Washington and British Columbia.

HABITAT: Often associated with *O. polyacantha* on rocky hillsides, frequently in shaded situations; in oak and yellow pine belts.

*OPUNTIA POLYACANTHA* Haworth, Suppl. Pl. Succ. 82. 1819. LaSal, San Juan Co., Moab, Grand Co.; Blanding and Montecello, San Juan Co., Kanab, Kane Co.; Zion National Park, Washington Co.; St. George, Washington Co. (1872); Fruita, Wayne Co.; in grassland between Hanksville and Green River. A common species in several western states from Nebraska and North Dakota to northwestern Oklahoma and Texas, from Arizona north to Alberta. Arizona and Utah are apparently the western limit.

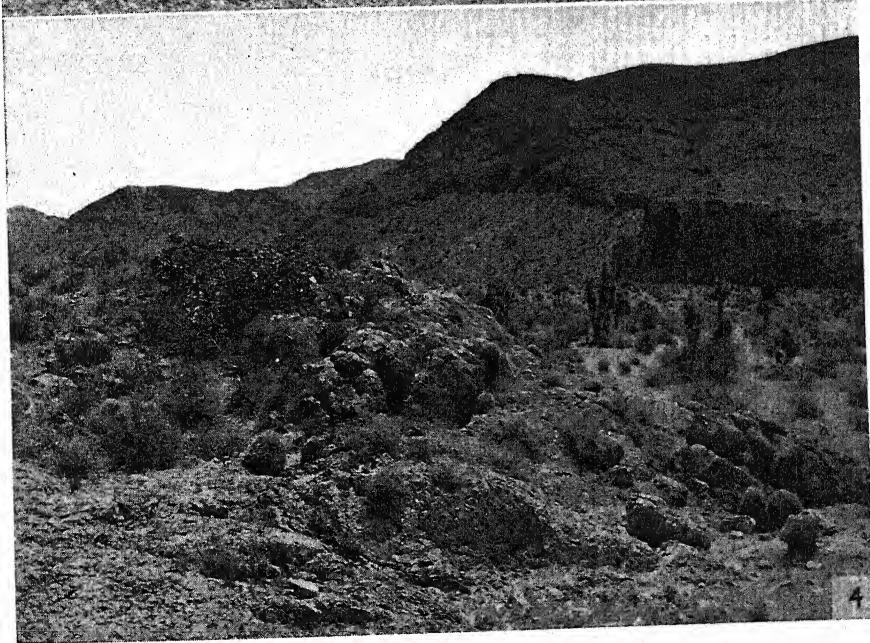
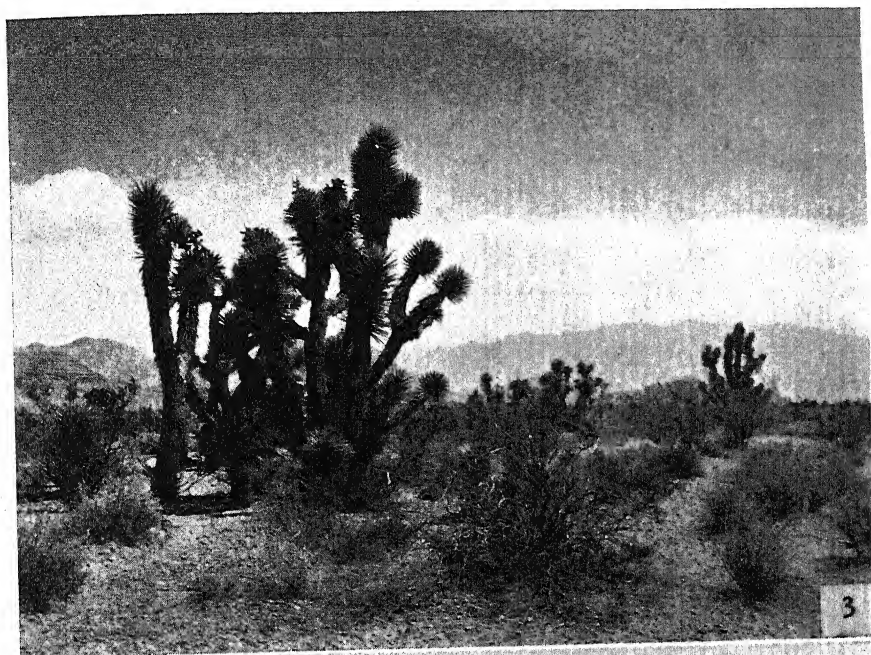
HABITAT: Sandy soil on desert plains, where it flourishes to the point of becoming a menace to ranchers; rocky hillsides often in juniper forests or associated with yucca. The flowers of this species not only vary from yellow to orange but are often magenta. This has caused some confusion, especially since Britton and Rose give the color of the flower as lemon yellow. The author has seen these plants in bloom on the Colorado plains with both yellow and magenta flowers on the same plant. An instance is known where scientific work was being carried on presumably with two species. The plant with magenta flowers was called *O. rhodantha* and the yellow flowered one, *O. polyacantha*.

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#### Explanation of Plate 16

Fig. 3. Joshua Forest, southwest of St. George, Washington Co., Utah. A subtropical cactus flora extends over this area.

Fig. 4. *Ferocactus acanthodes* and *Echinocereus Engelmannii* are in the foreground; *Opuntia echinocarpa* and Joshua trees are in the background.



CLOVER: CACTACEAE

*OPUNTIA RHODANTHA* Schumann, La Semaine Hort. 1897. Zion National Park, Washington Co.; Boulder, Garfield Co. (1889); Torrey and Fruita, Wayne Co. This species is found in western Nebraska, Colorado and Utah. Helen Dixon (Bot. Gaz. 97: 272-320) reported *O. xanthostemma* for the southern desert region in the vicinity of Torrey. It is probable that her specimen was *O. rhodantha* instead, since *O. xanthostemma* is a doubtful species. HABITAT: Plains, canyons and mountain sides, associated with sage-brush and piñon; also with aspen and yellow pine.

*OPUNTIA ERINACEA* Engelm., Proc. Amer. Acad. 3: 301. 1856. Montecello, San Juan Co.; Zion National Park, Washington Co.; St. George, Washington Co. (1895); Beaver Dam Mts.; Santa Clara Valley. Reported elsewhere from northwestern Arizona, southern Nevada, eastern California. The author has collected this species west of the Continental Divide in Colorado. It has been found frequently by Miss Carol Davidson who has collected in Colorado. HABITAT: Apparently confined chiefly to the Lower Sonoran Zone. On sandy plains and on limestone hills and ledges; associated sometimes with *O. polycantha* and with *Echinocerei*. It grows at a rather high altitude usually above 3500 feet.

*OPUNTIA TENUISPINA* Engelm. Proc. Amer. Acad. 3: 294. 1856. Specimens apparently correctly identified as *O. tenuispina* have been obtained from Zion National Park. This species was collected first in Zion National Park by L. A. Woodbury in 1930.

*OPUNTIA STENOCHILA* Engelm., Proc. Amer. Acad. 3: 296. 1856. Hanks-ville, Wayne Co. (1896). Hitherto reported from western New Mexico and northeastern Arizona. It resembles the common species of the eastern Mississippi Valley but is a lighter green, and has a slightly longer areole than the many specimens observed in the Middle West. HABITAT: Near the banks of the Dirty Devil River, sandy soil.

*ECHINOCEREUS MOJAVENSIS* (Engelm. and Bigelow) Britt. & Rose, Cact. 3: 8. 1922. Zion National Park, Washington Co.; Between Zion and St. George (1897); Joshua forest south of St. George; Upper Santa Clara Valley. This species is fairly abundant in western Arizona, southeastern California, Nevada and southwestern Utah. It has also been reported from Sonora. HABITAT: Limestone outcrops and sandy calcareous soil on hillsides, usually on south and west slopes. Associated in the vicinity of St. George with *E. Engelmannii*, *Opuntia basilaris*, *O. Bigelovii*, *Ferocactus acanthodes*, *Echinomastus Johnsonii* and *Phellosperma tetrancistra*, also with *Clistoyucca* (Joshua tree). Found in *Covillea* and *Artemesia* areas.

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#### Explanation of Plate 17

Fig. 5. *Ferocactus acanthodes*, a young plant showing the characteristic twisting of spines and the absence of hooks.

Fig. 6. *Coryphantha Marstonii* found on "Hell's Backbone," Boulder, Garfield Co., Utah. Type.





CLOVER: CACTACEAE

*ECHINOCEREUS TRIGLOCHIDIATUS* Engelm., in Wislizenus, Mem. Tour North. Mex. 93. 1848. LaSal, Grand Co. (1900). This cactus is found in western Texas, New Mexico, eastern Colorado and Utah. The author has seen specimens from the Uinta Mts., collected by E. H. Graham of the Carnegie Museum, Pittsburgh; L. A. Bradbury collected it on the Shewits Indian Reservation near St. George.

HABITAT: Limestone ledges in full light and sometimes under juniper trees partially shaded. Found also on flats in sandy calcareous loam.

*ECHINOCEREUS OCTACANTHUS* (Muhlenpfordt) Britt. & Rose, Cact. 2: 13, 1922. LaSal National Forest, Grand Co. (1898), Comb Wash, near Mexican Hat, San Juan Co.; Fruita, Wayne Co.; Common west of the Continental Divide, Colorado; the Uinta Mts., Utah; northern Texas and New Mexico. HABITAT: Limestone outcrops on ledges or hillsides. Abundant in Shavina Canyon, Montrose, Colorado. This species is unquestionably confused with *E. coccineus* which it closely resembles in form and habit. As far as the writer has observed from field studies in the western states *E. octacanthus* is much more abundant than *E. coccineus*, although, judging from the reports on distribution, the latter would seem to be.

*ECHINOCEREUS COCCINEUS* Engelm. in Wislizenus, Mem. Tour North. Mex. 94: 1848. Zion National Park; between Zion and St. George, Washington Co. (1884). This species has been found in the Uinta Mts. in western Colorado; and is reported from New Mexico and Arizona.

HABITAT: Calcareous soil, usually on ledges or hillsides; near Zion associated with *E. Engelmannii* and occasionally with *E. mojavensis*.

*ECHINOCEREUS ENGELMANNII* (Parry) Rumpler in Förster, Handb. Cact. ed. 2: 805. 1885. Mexican Hat, San Juan Co. (1878); Zion National Park; between Zion and St. George, (1880); Joshua forest south of St. George; Beaver Dam Wash; and Gunlock and Veyo, Washington Co. Distributed elsewhere in California, Arizona, Nevada, Lower California, and Sonora.

HABITAT: Limestone ledges, rocky calcareous hillsides. This species seems to be able to thrive under less favorable conditions than other Utah Echinocerei, i.e., in more extreme desert conditions, and in poorer soil. Abundant in Joshua forest, often associated with *Covillea tridentata*. A specimen from Mexican Hat is said by Mrs. W. E. Nevills to have white flowers.

*ECHINOCEREUS FENDLER* (Engelm.) Rumpler in Förster, Handb. Cact. ed. 2: 801. 1885. Utah-Arizona border, Monument National Park (1879). This species has been collected in Texas, New Mexico, Nevada, Utah, Arizona,

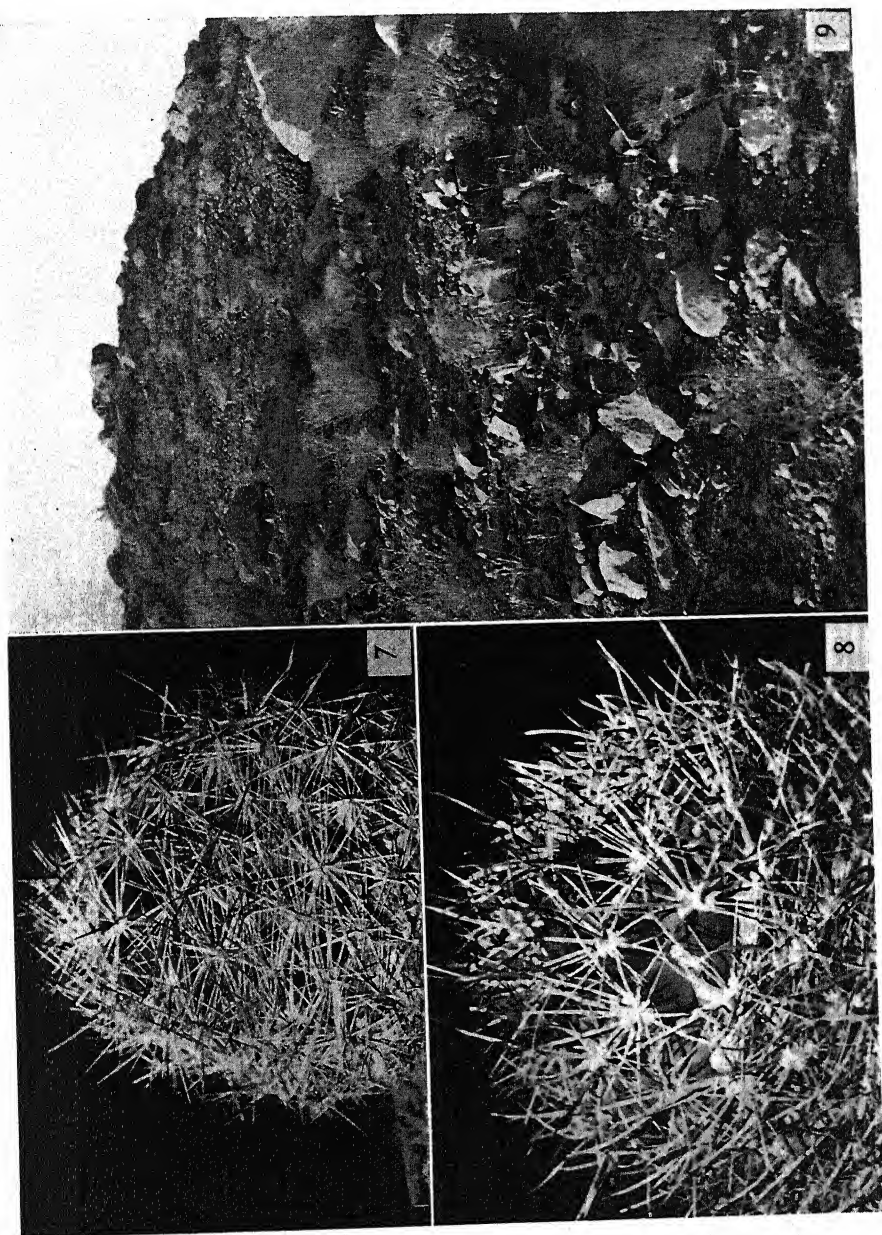
#### Explanation of Plate 18

Fig. 7. *Coryphantha* sp. nov. found between Veyo and Gunlock, Washington Co., Utah.

Fig. 8. *Utahia Sileri*. Near the Arizona-Utah<sup>1</sup> border, Fredonia, Arizona.

Fig. 9. *Echinocereus octacanthus* on a limestone hillside near Zion, Utah.





CLOVER: CACTACEAE

**HABITAT:** The plant is apparently extremely rare in Utah and difficult to find because its white spines blend so well with the light colored soil and limestone fragments among which it grows in the Joshua forest.

*CORYPHANTHA DESERTI* (Engelm.) Britt. & Rose, Cact. 3: 46. 1923. St. George, Washington Co. (1906). The range of this species has been extended the last few years; it is now known from southern California, southern Nevada, southern Utah and southwestern Colorado.

**HABITAT:** Desert areas in sandstone, among rocks, and on hillsides.

*CORYPHANTHA AGGREGATA* (Engelm.) Britt. & Rose, Cact. 4: 47-48. 1923. Blanding, San Juan Co. (1875). Distributed in western New Mexico, southeastern Arizona and along the Colorado River, southwestern Colorado, southern Utah and Sonora.

**HABITAT:** Found at Blanding in piñon and cedar area, limestone hills.

*CORYPHANTHA CHLORANTHA* (Engelm.) Britt. & Rose, Cact. 4: 43. 1923. East of St. George, Washington Co. (1907); known also from western Arizona, central Nevada and reported from southern California.

**HABITAT:** Hillsides, in red sandstone and often among rocks.

*CORYPHANTHA ECHINUS* (Engelm.) Britt. & Rose, Cact. 4: 42. 1923. LaSal National Forest, San Juan Co. (1874). The range of this plant is recorded far south of Utah, and it is surprising to find it so far north of its known habitat. The species has apparently been reported only from western Texas. Since the part of New Mexico, Utah and Arizona lying between these two regions are difficult to botanize thoroughly, it is possible that the plant has a wider distribution than we think. Two caespitose specimens were found.

**HABITAT:** Limestone hills, at LaSal, associated with *Opuntia fragilis*, *O. Phaeacantha*, *O. polyacantha*, on a hill sparsely covered with pines.

*CORYPHANTHA ARIZONICA* (Engelm.) Britt. & Rose, Cact. 4: 45-46. 1923. This species was not collected but was seen growing in gardens in the vicinity of St. George and was reported to have been collected locally. It has been found in northern Arizona, at Pipe Springs and near Cima and Goffs, California. Specimens closely resembling it were found by Miss Carol Davidson and the author in southwestern Colorado.

**HABITAT:** On hills, growing at a rather high elevation.

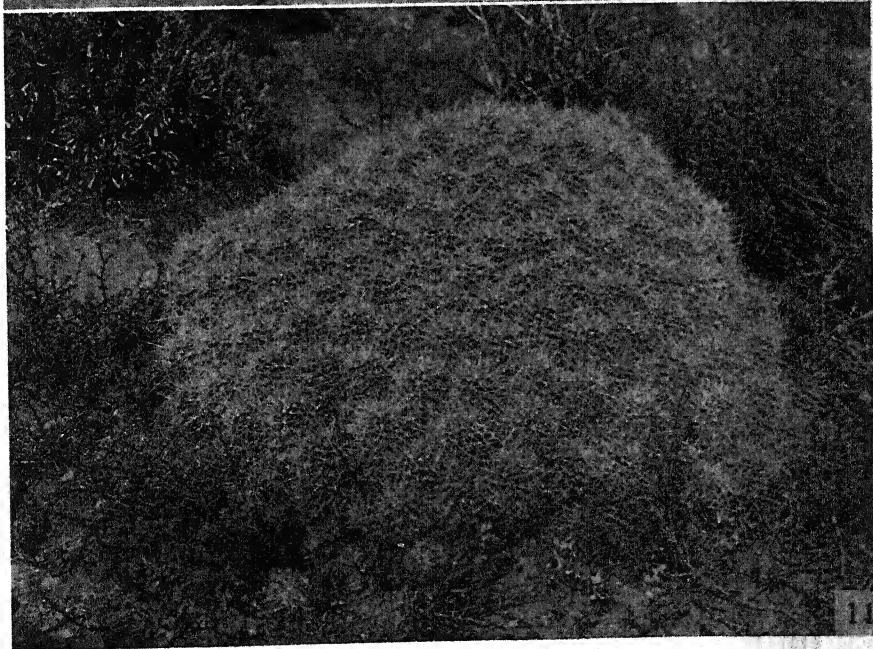
*Coryphantha* sp. nov.

Between Veyo and Gunlock, Washington Co. (1908). One healthy, and two dying specimens were found on a hillside in red sandstone strewn with granite fragments, associated with *Artemesia* and stunted *Covillea tridentata*. The

Explanation of Plate 19

Fig. 10. Limestone outcrop in sandstone north of Moab, Grand Co., Utah. *Juniperus utahensis* and *Artemesia* are dominant. Unhealthy plants and skeletons of *Sclerocactus Whipplei* and *Opuntia polyacantha* are found here.

Fig. 11. *Echinocereus octacanthus* at the base of cliffs between Montecello and Moab.



CLOVER: CACTACEAE



plant in some ways fits the description of *C. deserti*. The spines, however, are coarse and have a decidedly purplish cast, becoming black at the tip; radial spines never more than fifteen, centrals four; while *C. deserti*, according to the original description has a total of from twenty-five to thirty. Only dried flowers were available, and they appear to be yellow. The fruit is rather large, greenish purple and has a taste not unlike that of a ripe paw-paw (*Asimina*). Because of the meagre amount of material the author does not feel justified in naming this plant even as a new form until it is seen in flower.

***Coryphantha Marstoni* sp. nov.** Caespitosa, caulibus 4.5–6.5 cm. crassis; depresso-globosa; tuberculis sub-prismaticis, summis floriferis tomentosis sulcatis; junioribus dense lanatis; areolis 1.5 mm. latis, rotundis; spinis laterilibus radiatis, superioribus 4–5, setaceis rectis, albidis, inferioribus 9–12 radiantibus, rigidis, paullo recurvis, vel translucentibus pallide luteisque vel fuscis; 10–12 mm. longioribus, centralibus 2 vel 3, fuscis, apice nigris, inferiore (ex areolae centro) subulato, porrecto, 8–10 mm. longo; superioribus 12–15 mm. longis, rectis, obliquiter radiantibus; omnibus spinis basi bulbosis; floribus parvis, in plantae apice, 2 cm. longis, luteis, stigmatis lobis 5; filamentis numerosis; antheris luteis, fructibus ignotis. Utah. Specimen typicum (1909) vivum ex loco "Boulder" dicto conservatum est in Horto Botanico Universitatis Michiganensis.

Plant caespitose, forming a low flat clump with a stout tap root 2.5–3 feet long; stems crowded so that they are misshapen, depressed-globose, 4.5–6.5 cm. in diameter; tubercles sub-prismatic, about 1 cm. long, 4–5 mm. in diameter at base, very slightly less at tip; groove not extending to the base in all the older tubercles, lower end filled with whitish wool; aerioles circular, younger ones white-wooly; radial spines of two kinds, a tuft in upper end of areole, white, sometimes brown tipped, almost hair-like, somewhat shorter than other radials, these 9–12, rigid, acicular, uneven, the longest 10–12 mm. long, slender, horn-colored to light brown with darker tips, becoming grayish with age, radiating, occasionally slightly recurved, centrals usually 3, one in the center of the areole, subulate, porrect, with a swollen base, usually less than 1 cm. long, stouter than the other spines, red-brown to almost black at the tips; 1 or 2 upper centrals swollen at the base, similar in color to first central, rigid, acicular, ascending, pointing slightly outward, 12 to 15 mm. long; spines interlocking, forming rather a dense covering; flowers formed at base of tubercles at the apex, about 2 cm. long, yellow; style extending far beyond the stamens, stigma lobes 5; flower described from a dried specimen.

***Distribution:*** Known only from the type locality, "Hell's Backbone," a mountain ridge near Boulder, Garfield, Co., Utah (1909). Papers from the Department of Botany and the Botanical Gardens, University of Michigan, no. 645.

UNIVERSITY OF MICHIGAN,  
ANN ARBOR,  
BOTANICAL GARDENS AND ARBORITUM

## Response of sorghum to high and low soil moisture\*

V. PANDURANGA RAO

(WITH TWO FIGURES)

The grain sorghums are prominent among cereals of semiarid regions throughout the world. So far studies on sorghums have been largely confined to their morphology, genetics, and taxonomy. Only a small fraction of the voluminous literature on crop production is devoted to the highly important subject of roots and absorptive processes. That roots are the "least known, least understood, and least appreciated part of the plant" is particularly true of sorghums.

In India, sorghum is grown in a semiarid region characterized by low and irregularly distributed rainfall. Normally most of the rains fall as heavy downpours of as much as three to four inches in one day. During the last 30 years at Bellary, South India, dry cycles have occurred at intervals of four to five years with departures of six to eight inches below the 20-inch norm. Sorghum is the only grain crop that can be grown successfully under these conditions. It is also grown as a garden crop under irrigation. Hence, there is an urgent need for studying the response of this crop to widely different soil moisture content. There is little information on the subject of the response of roots of grain crops to wet and dry soils (Weaver and Clements, 1938).

### MATERIAL AND METHODS

*Sorghum cernuum* Host, was the species used in this experiment. Screened, fertile loess soil having a wilting coefficient of about 13 per cent was secured. It was divided into two lots which were adjusted to uniform moisture contents of 33 per cent (wet soil) and 14.8 per cent (dry soil), respectively.

Eight cylindrical galvanized iron containers 75 cm. deep and 28 cm. in diameter were used. A circular hole 6.5 cm. in diameter was cut in the middle of the side of each cylinder. These holes were corked while each of the two lots of soil was tamped uniformly into four containers. Lids were sealed on the completely filled containers with water-proof adhesive tape. Then the cans, each containing about 110 pounds of soil, were horizontally embedded in soil so that only the corks remained uncovered.

After removing the corks, three seeds were planted in each hole, and a thin layer of sand was added to reduce evaporation from the opening. The soil on the greenhouse bench between the containers was also planted to sorghum in order to provide conditions of competition for light similar

\* Contribution from the Department of Botany, University of Nebraska, No. 106.

to those encountered in the field. Light watering until the seedlings were four days old permitted germination and establishment in the dry soil. At this time, the plants were thinned to one per container.

During the experiment, the average temperature of the soil in which the plants were rooted was 56° F. and the air temperature varied between 65° and 75° F. The short light period of the winter days was extended until 10:00 p.m. by the use of two 150-watt electric lights mounted in 15-inch, white, enameled reflectors placed 3 feet above the containers. These were also used on cloudy days. The intensity of the light thus provided at 7:00 p.m. was 38 foot candles as compared with 3,000 foot candles at midday. Average daily evaporation from Livingston's black spherical atmometers was 11.6 cc., and relative humidity ranged from 55 to 60 per cent.

At the end of 42 days, the walls of the containers were cut open and the root systems washed free of soil. The volume of the roots was obtained by displacement of water in a graduated cylinder after they had been pressed between paper towels to remove surface water. The root systems were then floated out in deep pans of water in approximately the position occupied in the phytometer. Calculation of the total area of the root system selected as average was based on the total number and length of roots and the average diameters, as measured with the compound microscope and micrometer scale. Root hairs were thus excluded. This method was developed by Weaver *et al* (1924). The typical root system selected was also drawn to scale on cross-ruled paper while it was floating in its natural position over black paper ruled in square centimeters. The areas of above-ground parts were measured by first making prints on solio paper of the flattened leaves and stems and then using a planimeter. Finally, roots and tops were weighed after drying them at 90° F. for 24 hours.

## RESULTS

### *Plants Grown in Moist Soil*

The plants grown in moist soil, as measured to the tip of the youngest leaf, were 25.9 cm. tall and had stems 15 cm. long. The eight leaves had a surface area—upper and lower combined—of 299.7 sq. cm. (table 1). The ratio of shoot area to root area (excluding root hairs) was 1.95:1. The dry weight ratio, similarly, was 2:1. There were present 10 primary roots (fig. 1) which ranged from 8.6 to 42.0 cm. long and had a combined length of 265.2 cm. They were white and very turgid. Their diameters were between .25 and 1.0 mm. and averaged .725 mm.

The area of the primary roots (47.35 sq. cm.) constituted 30.9 per cent of the area of the entire root system. Arising from the primaries were



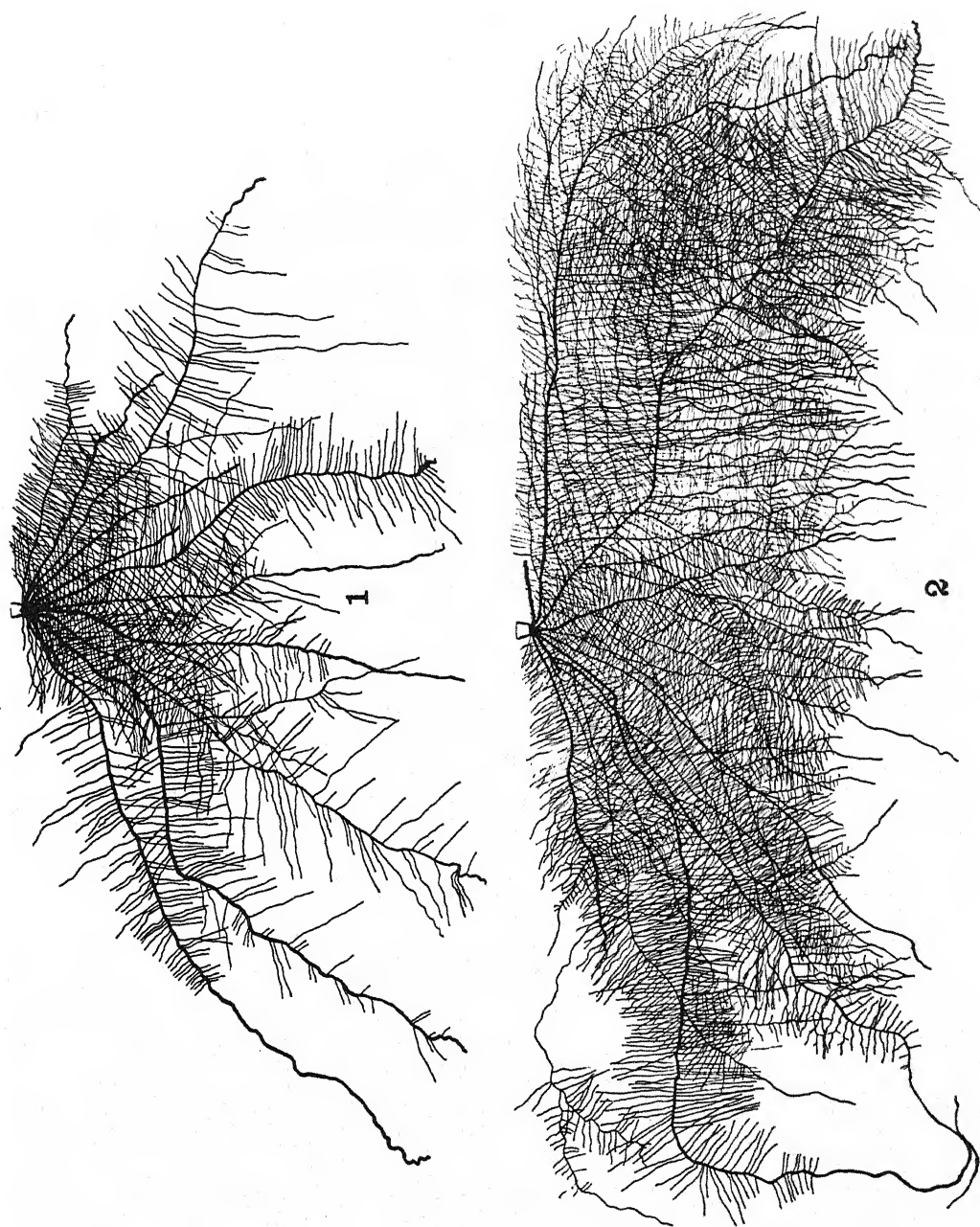


Fig. 1. Root habits of sorghum plants. Plants grown in (1) moist soil, and (2) dry soil,  $\times 4$ .

758 short, white secondaries with a total length of 1,178.6 cm. and an area of 90.7 sq. cm. or 59.3 per cent of the total area. Roots of the third and fourth order provided 9.1 and .7 per cent, respectively, of the total area (153 sq. cm.) of the root system.

TABLE 1

*Response of 42-day-old sorghum plants to high and low water content*

CRITERIA	MOIST SOIL 33 PER CENT MOISTURE	DRY SOIL 14.8 PER CENT MOISTURE
Height of plant, cm.	25.9	21.0
Number of leaves	8	8
Photosynthetic area of tops, sq. cm.	299.67	222.34
Dry weight of tops, gram	0.317	0.252
Dry weight of roots, gram	0.153	0.246
Volume of roots, cc.	1.25	1.84
Number of primary roots	10	8
Number of secondary roots	758	1,007
Number of tertiary roots	470	1,952
Number of quaternary roots	101	354
Total number of roots	1,339	3,321
Length of primary roots, cm.	265.2	328.0
Length of secondary roots, cm.	1,178.6	3,017.9
Length of tertiary roots, cm.	415.8	2,649.5
Length of quaternary roots, cm.	51.0	177.0
Total length of root system, cm.	1,910.6	6,172.4
Absorbing area of primary roots, sq. cm.	47.35	57.40
Absorbing area of secondary roots, sq. cm.	90.70	265.60
Absorbing area of tertiary roots, sq. cm.	13.85	116.60
Absorbing area of quaternary roots, sq. cm.	1.13	3.90
Total absorbing area of roots, sq. cm.	153.03	443.50
Number of root hairs per unit length	33.0	83.4
Average length of root hairs, $\mu$	229	136

The root hairs constituted by far the best absorptive agency of the plant. It was practically impossible to measure their total area because of their minuteness and abundance. However, microscopic determinations of their length and general distribution were made at different levels of the root system. The average number of root hairs per unit length (700 $\mu$ ) at fifty different levels was 33, with a maximum (in any unit length) of 41 and a minimum of 26. Only those root hairs visible on either side of the root when viewed through the microscope were counted. The average length of root hairs, determined from 500 readings at different levels in

all roots, was  $229\mu$ , the distribution in length varying from  $525\mu$  to  $105\mu$ .

The average volume of the root systems of four plants was 1.25 cc., the average dry weight .153 grams.

### *Plants Grown in Dry Soil*

The plants grown in soil with approximately 1.8 per cent available moisture had eight leaves when 42 days old. They were 21 cm. tall and had stems 12.5 cm. long. The surface area of the shoot was 222.34 sq. cm., that of the root system 99 per cent greater. The average dry weight of tops was .252 gm. (table 1). The ratio of dry weight of tops to that of roots was 1.02:1.

The eight primary roots ranged in length from 2.5 to 130.7 cm. and had a combined length of 328 cm. The longest one consisted of a main root and six branches from its tip. These eight roots varied in diameter from .25 to 1.0 mm., the average being .5 mm. They were light brownish yellow in color. The area of the primary roots (57.4 sq. cm.) was 12.9 per cent of that of the root system.

There were 1,007 secondary roots with a total length of 3,017.9 cm. They were discolored like the primaries. Their area of 265.6 sq. cm. was 59.9 per cent of that of the root system. The 1,952 tertiary roots had a combined length of 2,649.5 cm. and an area of 116.6 sq. cm. This was 26.3 per cent of the total area and with the area of the secondaries composed 86.2 per cent of the total. The 3.9 sq. cm. area of the quaternary roots was distributed among 354 roots with a total length of 177 cm. This was .9 per cent of the whole 443.5 sq. cm. area of the root system.

The average number of root hairs per unit length of  $700\mu$  taken at fifty different levels was 83.4, and ranged from 68 to 118; their average length, as obtained from 500 measurements at different levels in all roots, was  $136\mu$ , the length varying from 70 to  $287\mu$ .

Average dry weight and volume of the root systems were .246 gm. and 1.84 cc., respectively.

### DISCUSSION

Comparison of the foregoing data shows that low soil moisture content inhibited the growth of the shoot of sorghum while increasing the number and length of all orders of roots (except number of primaries). The primary roots were 1.24 times longer, secondaries 2.57 times, the tertiaries 6.37 times, and roots of the fourth order 3.47 times longer than those of moist soil. There were 1.33 times more secondaries, 4.15 times more tertiaries, and roots of the fourth order were 3.5 times more numerous. Stated conversely, moist soil favored the growth of tops and primary roots but

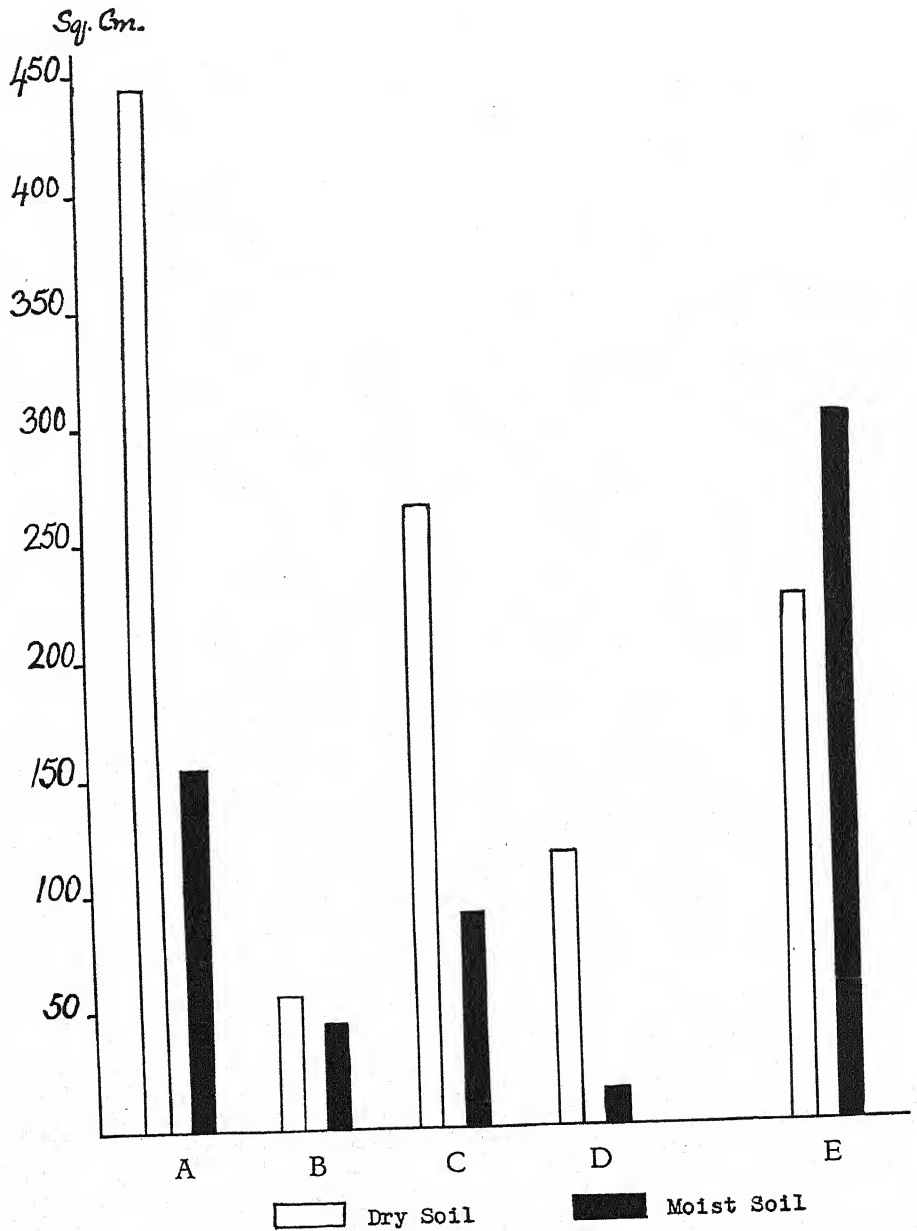


Fig. 2. Graph showing the relationship between: A, the area of the entire root system; B, the area of the primary roots; C, the area of the secondary roots; D, the area of the tertiary roots; and E, the photosynthetic and transpiring areas of *Sorghum* plants grown in dry and moist soil.

checked that of secondary, tertiary, and quaternary roots. The total length of the roots in dry soil (6,172.4 cm.) was 3.23 times as great as in plants grown in moist soil, and the root area in the former was 2.9 times that in the latter. In dry soil, root hairs were more numerous (83.4 per unit of length) and shorter ( $136\mu$ ) than in moist soil where the number was 33 and the length  $229\mu$ .

It is noteworthy that the dry soil dwarfed the shoot while accentuating root development (fig. 2). This tends toward an equilibrium between absorption of water and its loss in transpiration. In a similar study but using a more mesic species, Weaver and Clements (1938) found that "Corn grown for 5 weeks in a moist, rich, loess soil (available water content 19 per cent) had a total root area which was 1.2 times greater than that of the transpiring surface of stems and leaves. Similar corn grown with an available water content of only 9 per cent had a root area 2.1 times greater than that of tops . . . Thus, a low water content, within certain limits, stimulates increased root development" of maize. Most of the increased absorbing area was furnished by "an excellent development of secondary and tertiary branches."

In this experiment, the root area of sorghum in moist soil was much less than the photosynthetic area, but in dry soil it was double the photosynthetic area. The primary roots in the dry soil were thinner and longer and constituted only 13 per cent of the total root area, whereas those in the moist soil were thicker and shorter and composed 31 per cent of the area of the root system. In moist soil the primaries and secondaries dominated, but in dry soil the secondary and tertiary roots provided the largest area. The capacity of the plant to elaborate its root system and at the same time to meet the stress of drought by limiting the development of its shoot is especially noteworthy (fig. 2).

#### SUMMARY

Sorghum plants were grown for 42 days in soils with 33.0 and 14.8 per cent moisture of which only about 20 and 1.8 per cent, respectively, were available for growth, *i.e.*, above the hygroscopic coefficient.

Plants grown in moist soil were one-fourth taller and heavier and had one-third more photosynthetic area than those grown in dry soil. In moist soil the dried tops were twice as heavy as the roots but in dry soil the weight of tops and roots was the same. Haasis (1921), and Crist and Stout (1929) also found that the dry weight ratio of shoot to root is proportional to available soil moisture. The plants grown in dry soil had more and longer roots and nearly three times the area of those in moist soil.



Under both treatments, well developed secondary roots were produced. The moist soil proved more favorable to the development of primary roots, but the tertiaries were better in dry soil. Volumes of root systems in the moist and dry soils averaged 1.25 cc. and 1.84 cc., respectively. In the latter, root hairs were more abundant but shorter. Dryness of soil stimulated root growth considerably and inhibited the growth of above-ground parts.

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## Raymond H. Torrey

JAMES MURPHY

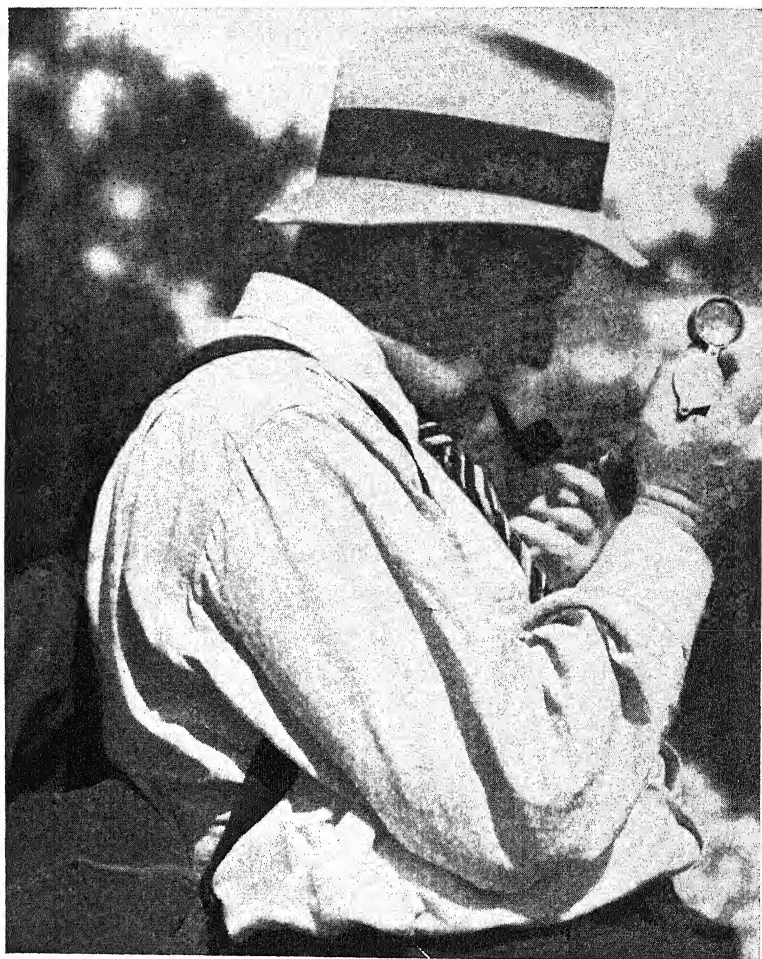
RAYMOND HEZEKIAH TORREY was born in Georgetown, Massachusetts, on July 15th, 1880. He died in New York City, July 15th, 1938, his 58th birthday. He was the son of Grafton F. Torrey and Leonora Warren, both of whom were born at Deer Isle, Maine.

On his father's side he was related to John Torrey, the American botanist. His mother was a descendant of Richard Warren, who landed at Plymouth on the "Mayflower," and of General Joseph Warren, who was killed at Bunker Hill. His father and uncles were all seafaring men, and from them, as a boy, he heard many tales of adventure and distant places, which left a very vivid impress on his memory. He was a life member of the National Society of Puritan Descendants.

His early education was received in Georgetown. While in grammar school he became acquainted with Mr. and Mrs. Horner, local botanists, who were employed by Harvard College to collect specimens for use in classes in botany. Mr. Torrey frequently went with them after school and on weekends in search of specimens, and it became necessary in the pursuit of some rarer species to go even further and further afield due to their disappearance as a result of indiscriminate collecting. It was this fact that first directed Mr. Torrey's attention not only to tramping out-of-doors, but particularly to the urgency of the conservation and protection of our native flora. His interest in botany was further stimulated by his instructor in high school.

Upon graduation from the Georgetown High School in 1896, he obtained employment in the local newspaper, performing the varied tasks of editor, reporter, typesetter, and on occasion operated and even tended to and stoked the steam boiler which supplied the power. This journalistic experience, however, aided him in obtaining a position on the "Springfield Union." In 1903 he came to New York and entered the employ of the New York City News Association, as assistant to the night city editor and was later engaged by the "New York American" and "Herald Tribune." On the two latter papers he attained the position of Night City Editor. He conducted a column in the "New York Post" for many years, until his death, under "The Long Brown Path," which was devoted to life out-of-doors and to scientific aspects of nature.

His interest in botany led him to become a member of the Torrey Botanical Club which he did in 1920. The numerous articles and notes in "Torreya" attest to his enthusiasm for botany, and particularly to those [THE BULLETIN FOR JUNE (65: 347-432) WAS ISSUED JUNE 20, 1938]



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boreal plants found on high elevations throughout the club area, which are generally considered glacial relicts.

In his later years, due to the encouragement and inspiration of Dr. Alexander W. Evans, his interest was aroused in lichens, particularly the genus *Cladonia*, in which the club territory is particularly rich in species, forms and modifications. As the fruit of his travels and studies he contributed to "Torreya" an article "Cladoniae in the Range of the Torrey Botanical Club," which was profusely illustrated and constitutes the principal source of scientific knowledge and information on that subject available to those interested in the Cladoniae of this region. This was followed by other articles in "Torreya" on the same subject.

His native zeal and infectious enthusiasm stirred other students to an intensive pursuit of lichens generally, and particularly of the genus *Cladonia*. Prior to his death he had gathered together material for a memoir on the subject, with particular relation to the species *Cladonia Boryi* Tuck. which is found generally along the coast. The study was intended to embrace the area from Newfoundland to North Carolina as far as Nag's Head.

As a result of his apparently well-night indefatigable energy, as well as enthusiasm, he assembled probably the most complete herbarium of that genus in this part of the country, certainly the most complete in private possession.

He had been for sometime prior to his death the curator of the Cladoniae herbarium of the Sullivant Moss Society.

He eagerly looked forward to the time when he should be relieved of his other activities sufficiently to permit him to scientifically arrange the material collected and distribute it among those institutions which were interested therein. He had gathered together a library of practically all modern works on the subject, not only in English, but in French and German as well.

For the last eight years he was the chairman of the field committee of the Torrey Botanical Club, and the printed schedules of trips stand out as evidence of his devotion to outdoor botany. They have undoubtedly done much to maintain the tradition established and furthered by John Torrey and Nathaniel L. Britton.

Recognition of his efforts was manifested by his designation as a member of the Board of Managers of the New York Botanical Garden, and his election, this year, to the presidency of the Torrey Botanical Club.

While his work on Cladoniae has permanent scientific value, his efforts in the promotion of outdoor-life and conservation have contributed greatly

not only to the enjoyment of many, but also to the future welfare of this country.

His alert mind and imagination being no doubt attracted by the natural beauty of the New England country-side, he spent much of his time traveling and in fact climbed to most of the important peaks. To facilitate the enjoyment of these natural beauties, he, in co-operation with others, laid out many trails, and particularly did he help in realizing the Appalachian trail from Mt. Katahdin in Maine to Mt. Oglethorpe in Georgia.

Naturally, his particular interest was directed towards the trails in New York City, in which city he spent his entire adult life. At the time of his death he was the chairman of the New York-New Jersey Trail Conference, and he was the editor of the "Guide to the Appalachian Trail," from the Housatonic to the Susquehanna Rivers.

In conjunction with Mr. Frank Place, Jr. and Dr. Robert L. Dickinson he was author of the "New York Walk Book." This publication was well received, and a new edition has been published by Dodd, Mead & Co., in 1934.

Some years prior to his death he gave up newspaper work, in which he had been actively engaged, except "The Long Brown Path," and became the secretary of the American Scenic Historic and Preservation Society and of the Society for the Preservation of the Adirondacks. This work gave him the opportunity, which he had long desired, of effectively advancing the cause of conservation, particularly in the eastern part of the United States. There came under his direct supervision and control such scenic and historic monuments as John Boyd Thacher Park in the Helderbergs, the Stony Point Reservation on the Hudson, Philipse Manor Hall, Letchworth Park, including Portage Falls on the Genesee River, Diamond Island in Lake George, Battle Island Park on Oswego River, and for a time, Watkins Glen in the Finger Lake Region of New York State.

He was above all devoted to the preservation of the Adirondacks, and particularly the lands that constitute the "Forest Preserve" of New York State, which under the State Constitution (Article 7, Section 7) "Shall be forever kept as wild forest lands." By reason of repeated attempts to encroach upon this preserve, Mr. Torrey was kept constantly on the alert in defense of the Forest Preserve. Just before his death, he was particularly concerned, by reason of the fact that a proposed new Constitution was being drawn for the State, and, to him, it was of the utmost importance that present ARTICLE 7 in SECTION 7 should not be thereby impaired or limited in its original scope and intention.

This work of Mr. Torrey's was what gave him the greatest inner satisfaction, since he felt that in protecting our natural heritage from the selfish exploitation by man, he was contributing not only to the preservation and furtherance of the health and spiritual uplift of his contemporaries, but also of those who would come after him, for he had found for himself in this changing and troubled world, in his communion with nature, that salvation for which man ever strives.

In addition to his daily contributions to the newspapers, Mr. Torrey wrote numerous articles of botanical historic, and scenic interest, and especially those concerned with conservation. (See bibliography).

Besides his widow, he left a married son, Raymond, a married daughter, Leonore Torrey Millett, a grandson, Warren Millett, a brother, Warren, of Revere, Massachusetts, and a sister, Mrs. Raymond Jackson, of Grey-stone Beach, Marblehead, Massachusetts.

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## A large species of *Rhizophidium* from cooked beef

J. S. KARLING  
(WITH PLATES 20 AND 21)

In an experiment conducted to determine the host range of several species of *Rhizophidium* which occur on algae, flagellates, rotifers, etc., sterilized bits of ground beef were frequently used as one of the host media. Two of these chytrid species grew fairly well on this medium, and during the course of a study of their thalli a third member of the same genus appeared which at present seems to be different in many respects from any of the known species. With the infected bits of beef as a source of material I have been able to transfer this species to cooked filaments of *Cladophora glomerata*, *Pithophora* sp., *Nitella flexilis*, *Chara coronata* and root tips of *Allium cepa* and *Narcissus* sp. All attempts to grow it on living cells have so far given only negative results. This is the first report in the literature of the occurrence of a species of *Rhizophidium* on cooked ground beef, and such a habitat seems at first to be rather striking and unusual. When it is recalled, however, that other species of the same genus have been reported from dead rotifers, various animal eggs, nematodes, etc., this occurrence appears less remarkable.

The present species is characterized structurally by unusually large thalli, sporangia, zoospores, and resting spores; and with the object of emphasizing these characteristics I am accordingly proposing the specific name *macrosporum* for it.

***Rhizophidium macrosporum* n. sp.** Thalli eucarpic, numerous, gregarious. Zoosporangia hyaline, smooth, predominantly spherical 22–110  $\mu$ , oval, broadly pyriform, and urceolate with 1 to 5, usually 2 or 3, low inconspicuous exit papillae. Zoospores spherical 4.5–6  $\mu$ , hyaline, with an unusually large, 3–4  $\mu$ , clear refractive globule and a 25–35  $\mu$  long cilium; occasionally becoming amoeboid; initial swarmspores emerging in a small globular mass surrounded by a hyaline matrix and lying quiescent for a few moments before separating; the remainder becoming active within the sporangium and emerging usually one by one. Rhizoidal system usually extensively developed, coarse, and branched, main axis occasionally 6  $\mu$  in diameter; delimited from the sporangia by a cross wall at maturity; arising from a single point or rarely from several places at the base of the sporangium. Resting spores hyaline, smooth, spherical, 15–30  $\mu$ , oval, 18 $\times$ 20–33 $\times$ 36  $\mu$ , or slightly irregular with a wall 1.5–2  $\mu$  thick, and one or more large refractive globules; germination unknown.

Saprophytic on cooked ground beef, dead cells of *Cladophora glomerata*, *Pithophora* sp., *Nitella flexilis*, *Chara coronata* and root tips of *Allium cepa* and *Narcissus* sp., in New York City.

## STRUCTURE OF THE THALLUS

The thallus of *R. macrosporum* is usually very large and extensive. Figure 1 shows an exceptionally large individual from cooked beef with a sporangium which measured  $105\ \mu$  in diameter and whose rhizoidal system extended  $310\ \mu$  in a linear direction. It is thus obvious from this figure that species of *Rhizophidium* are not always small, but that their thalli may become as extensive as those of *Endochytrium*, *Diplophlyctis*, *Rhizophlyctis*, etc. The rhizoidal system of this species is usually richly branched with the extremities running out to fine tapering filaments and points. It usually arises at one point at the base of the sporangium or resting spores, as is shown in figures 1, 2, 3, 14, 15 and 16, but occasionally several axes may develop at separate regions on the base so that the sporangia become polyrhizoidal, figures 2, 4. Such thalli are doubtless formed from zoospores which develop more than one germ tube, as is suggested by figure 13. Sometimes the rhizoidal system consists of an elongated tapering tubular stalk or axis which branches extensively at its tip, so that the sporangia and resting spores become distinctly stalked, figures 3, 15. This stalk in exceptional cases may attain a diameter of  $6\ \mu$ . In all thalli which I have been able to observe with clarity on bleached and semi-transparent host material the rhizoidal system was distinctly delimited from the sporangia by a cross wall.

The sporangia are usually sessile, but when they are crowded in groups some may stand off at varying distances from the surface of the host on the rhizoidal stalk. They may vary considerably in size, and as has been noted in the diagnosis given above the largest ones so far found on beef measured  $110\ \mu$  in diameter. Other spherical ones have been observed on *Cladophora glomerata* and beef which measured only 22 and  $23\ \mu$  respectively. The majority, however, are much larger according to present observations. Figures 2 and 4 show somewhat urn-shaped sporangia from *Cladophora* and *Chara*, while figure 3 illustrates one from *Nitella*. At maturity the refractive globules are so large and numerous that very little of the remaining protoplasm is visible in the sporangium, as is well shown in figures 1 to 4. The exit papillae are usually rather low and inconspicuous and vary from 1 to 5 in number. Usually only two or three are present and may be located apically or subapically.

The method of zoospore emission is similar to that of other species of *Rhizophidium* with the exception that the initial mass of emerged zoospores is usually rather small, and in the individuals separate and become motile very shortly. One or more of the exit papillae deliquesce at the same time, and a globule of hyaline fluid or slimy matrix issues forth. A few zoospores, 5-10, escape into this globule and lie quiescent for a few

moments. As the globule dissolves in the surrounding water the swarmspores begin to separate and soon dart away. Others emerge successively, pause for a few seconds at the orifice, and then become actively motile. Sometimes the diameter of the orifice, may be smaller than that of the zoospores, so that the latter must elongate to emerge. As the pressure in the sporangium is apparently reduced those within begin to glide upon each other, and in a few seconds thereafter they are swarming violently inside of the sporangium. Those which fail to escape may remain motile for as long as two hours. Eventually they degenerate or germinate in situ. In some cases such trapped zoospores may increase markedly in size before germinating or disintegrating. Figure 9 shows such a zoospore which measured  $12\ \mu$  in diameter. Its refractive globule has also increased to a diameter of  $10\ \mu$ . After the zoospores have escaped the sporangia may collapse partly and become greatly wrinkled.

As has been noted above the zoospores are hyaline and spherical,  $4.5\text{--}6\ \mu$ , with a  $25\text{--}35\ \mu$  long posterior cilium. The refringent globule is frequently so large that it appears to constitute the major part of the spore. It is hyaline and refractive, and as the swarmspores become amoeboid and creep about in tight places it may undergo marked changes in shape, figures 6, 7, 8, showing that it is quite plastic in consistency. The motility of the zoospore is typical of other species of this genus. They dart about very quickly, come to rest momentarily, then dash away again. They may occasionally become amoeboid as is shown in figures 6, 7, 8, but this tendency is not as pronounced as in *R. sphaerocarpum*.

Germination of the swarmspores in water is not uncommon as is shown in figures 10, 11, and 13. The germ tube however, is not particularly thick for such large zoospores, according to present observations. Occasionally two and three tubes may develop, and such spores doubtless give rise to polyrhizoidal sporangia and resting spores. During the course of this study another smaller species of *Rhizophidium*, which is to be described below, infected the same host material, and the two were frequently found side by side. Inasmuch as the sporangia were often similar in appearance and the zoospores swarmed together, the suggestion immediately arose that I might be dealing with a heterothallis species with sporangia and motile gametes of marked difference in size. Careful watch was therefore kept for possible conjugation stages. Quite often the zoospores came to rest side by side, figure 13, but no fusion occurred. In other instances the germ tube of the smaller swarmspores was found growing towards the larger one as in figure 12. This suggested the possibility of fusion through a conjugation canal, but from careful observation of a number of such cases I am convinced that this orientation of the

germ tube is merely fortuitous and of no significance sexually. The smaller zoospores doubtless relate to another species.

The development of the sporangia is not fundamentally different from that of other species of *Rhizophidium*, with the exception that the amount of refractive substance is more abundant. This was at first believed to be associated to some degree with the type of host medium used, but since the refractive globules are just as large when the sporangia occur on alga cells this is apparently not a vital factor.

#### RESTING SPORES

The resting spores of *R. macrosporum* have so far only been found on cooked and degenerating bits of beef. They are hyaline, smooth, predominantly spherical,  $15\text{--}36\ \mu$ , and oval,  $18\times 20\ \mu\text{--}33\times 37\ \mu$ , but occasionally somewhat obpyriform, and irregular ones occur. They usually possess a very large refractive central globule, which in the largest spore so far found measured  $30\ \mu$  in diameter. The large globule may often be surrounded by a number of smaller ones as is shown in figures 15 to 17. Occasionally two or more fairly large globules may be present, figure 15. The wall is not particularly heavy for spores of this size and does not usually exceed  $2\ \mu$  in thickness. The spores are predominantly monorhizoidal, but sometimes stalked, figure 15, and polyrhizoidal ones occur, figure 17.

According to present observations these resting spores develop in the same manner as the evanescent zoosporangia up to a certain stage. After that they may usually be recognized by an abundance of large refringent globules as is shown in figure 14. With further development these apparently coalesce to form the large central one which is so characteristic of the mature spores, while the wall begins to thicken. So far no evidence of sexuality has been found in their development, nor has germination been observed.

***Rhizophidium* sp.**—During the course of my study of *R. macrosporum* described above, another species of the same genus was found on dead rotifers, exuviae of various insects, and cysts of several unicellular algae which had been collected in a pond on Dr. R. A. Harper's farm near Ridgewood, N. J. In the shape of its sporangia and size of zoospores it may frequently resemble *R. agile*, *R. gibbosum*, and *Phlyctochytrium bisporum*.

This species was first observed on various dead animal and algal hosts, and with this as a source of material extensive cross inoculation experiments have been made to determine the range of host tissues upon which it will grow. It soon proved to be ubiquitous and capable of infecting and

growing saprophytically on a wide variety of material. Among plants it has been grown on killed cells of *Cladophora glomerata*, *Pithophora* sp., *Oedogonium* sp., *Spirogyra crassa*, *Nitella flexilis*, *Chara coronata*, *Hydrodictyon reticulatum*, and root tips of *Allium cepa*, *Zea mays*, *Pisum sativum*, *Narcissus* sp., *Triticum* sp., and *Avena sativa*. On root tips the thalli occur abundantly over the cap and formative region, and in heavily infected roots as many as 25 sporangia have been counted per sq. mm. of surface.

Among the algal and vegetable debris in which this chytrid occurred were numerous flagellates, rhizopods, rotifers, and other small animals. In the course of time many of these died and became infected. I have accordingly found it growing on dead individuals of *Phacus pleuronectes*, *Euglena viridis*, *Arcella vulgaris*, *Arachnula* sp., *Diffugia urceolata*, *Centropyxis* sp., *Euglypha* sp., *Monostyla* sp., and *Distyla* sp. Its occurrence on such a wide variety of animals suggested at once that it might be grown on other host material of this type. Dead ova and ovarian tissues of *Fasciola hepatica* were added to my cultures and became heavily infected within a few days. In two bits of material the ovarian tissue was completely overrun with thalli. I have also succeeded in growing it on dead eggs and young larvae of *Drosophila melanogaster*, dead abdominal tissues of cockroaches and thoroughly cooked striated muscle cells of beef. Its growth on the latter was limited and sparse, and the thalli did not appear until the beef had degenerated rather thoroughly.

Concurrently with these experiments involving dead plant and animal material attempts were also made to grow this chytrid on living algae and animal tissues. So far the results have been negative so I am inclined to regard this species as a saprophyte. It is to be noted here that Zopf described *R. agile* and *R. gibbosum* as virulent parasites which caused a marked degeneration of the chlorophyll and the remaining protoplasm. In this respect our species differs markedly from those of Zopf.

#### STRUCTURE OF THE THALLUS

This species is quite gregarious, and as many as 65 thalli have been counted on a single liver fluke ovum. On larger cells such as internodes of *Chara* and *Nitella* several hundred thalli in various stages of development may be present, while on root tips the cap and formative region may sometimes be almost completely covered. When a large number of thalli are grouped together in a localized region on a host cell, as is shown in figure 18, the sporangia are usually small and triangular or irregular in shape, doubtless partly as the result of mutual contact and pressure. Sometimes the sporangia do not rest directly on the surface of the host



cell but stand off at varying distances on the rhizoidal stalk or axis. In a few instances this extramatrix stalk has measured 10 to 15  $\mu$  in length.

This size to which the thallus may grow is illustrated in figure 19 of an isolated specimen growing on a thin, almost transparent strip of ovarian tissue of *Fasciola hepatica*. The rhizoidal system extended for a linear distance of 197  $\mu$  and consisted of a long stalk, 4  $\mu$  in diameter, which branched several times at its lower extremity. The sporangium measured 45  $\mu$  in diameter and is almost spherical in shape, with eleven exit papillae distributed rather evenly over its surface. This is one of the largest specimens I have so far found, and may be regarded as representing the upper limits. The lower limit in size is shown in figure 20. This sporangium is only 12  $\mu$  in diameter, while the rhizoidal system extends only about 25  $\mu$  in linear direction.

The main axis or stalk of the rhizoidal system when present may vary considerably in diameter and length. Occasionally it may be short, inflated, and apophysis-like, as in figures 21 and 31. When the thallus shown in figure 21 was first observed on *Narcissus* root tips I believed it related to a species of *Phlyctochytrium*, but as I followed it through to maturation and the emission of its zoospore I became convinced that it belonged to *Rhizophidium* sp. Such thalli according to present observations are comparatively rare, but they none the less show that species of *Rhizophidium* may occasionally resemble members of *Phlyctochytrium* in the character of the intramatrix rhizoidal system. A few thalli of this nature with small intramatrix, apophysis-like swellings on the rhizoidal system have also been reported by Zopf (1888, pl. 20, fig. 19) and Morini (1896, fig. 2) for *R. gibbosum* and *R. messanense* respectively.

The central stalk or axis may often be very short or lacking entirely, and in such cases a number of rhizoidal branches arise at the base of the sporangium as is shown in figures 24 and 30. These branches may often be very fine in the small thalli so as to form a brush-like tuft, while in the larger ones they may be relatively coarse.

The mature sporangia also vary considerably in shape and size. They may be almost spherical, 10–52  $\mu$ , slightly depressed, wedge-shaped and somewhat triangular, 14 $\times$ 29  $\mu$ –25 $\times$ 30  $\mu$ , oval and occasionally slightly irregular. The exit papillae are usually very low and vary from 1 to 11 in number. Sporangia with a single papilla as well as those with a high number are comparatively rare. Two to four appear to be the most common numbers according to present observations. The highest number of papillae usually but not always occur on the larger sporangia. The orifices for the emission of the zoospores vary from 3 to 5  $\mu$  in diameter and are usually slightly oval or spherical.



In mounting the host tissue for study sporangia often break away from the rhizoidal system and lie free in the surrounding water. Occasionally the main rhizoidal axis or stalk accompanies them, figure 33. These sporangia are quite normal in appearance, and if mature they may undergo cleavage and emit their zoospores in the usual manner. Their ability to break away and develop thus is doubtless due to the fact that they are delimited from the rhizoidal system by a cross wall.

At maturity the protoplasm of the sporangia is relatively homogeneous optically, except for a great number of minute globules which do not appear to be refringent as those of other *Rhizophidium* species. This difference may be due largely to their small size, since they usually measure less than  $1\ \mu$  in diameter. Figure 22 shows the appearance of a sporangium with two subapical exit papillae approximately two hours before dehiscence began. Whether or not cleavage has occurred is not certain, but the limits of the individual zoospores are not yet visible. A short while before the sporangium opens, however, the lines of demarcation usually become quite distinct. Often the distinction may become as clear and sharp as Couch (figs. 59, 60) has shown in *P. bisporum*. Since the thalli occur in such great abundance it is not difficult to find sporangia in all stages of dehiscence. Several exit papillae may deliquesce at the same time, so that the swarmspores may be seen emerging at several places on the sporangium. Sometimes they emerge one by one, become momentarily amoeboid and swim directly away, figure 23. In other cases a number of spores may emerge in a small globular mass surrounded by a hyaline matrix and lie quiescent for a few moments before loosening up and moving apart, figure 24. From present observations I believe the latter type of behavior is the more normal and usual for the very large sporangia of this species. Numerous factors, however, such as unfavorable environmental conditions, premature deliquescence of the exit papillae etc., undoubtedly influence the process and lead to variations. I have not so far observed the initial globular mass of extruded zoospores to become as large and conspicuous as Zopf describes for *R. sphaerocarpum*. This may perhaps be due in part to a difference in viscosity of the surrounding matrix. After a considerable number of zoospores have emerged the pressure in the sporangium is apparently reduced, so that the remaining spores soon become active. They first begin to glide slowly upon each other, but after a few seconds they attain such motility that the sporangium becomes a mass of seething and darting spores. These then emerge one by one, in twos, or in threes. By observing only this stage one might readily get the impression that it constitutes an initial stage of zoospore emission. The length of time required for total emission is rather short, varying from

50 to 200 seconds, according to the size of the sporangium. Occasionally a number of zoospores may fail to escape and these either degenerate or germinate in situ. The empty sporangium usually becomes somewhat shriveled and wrinkled, and may often take on a yellowish brown tinge with age. Extensive tests with chloriodide of zinc on the walls have so far failed to give any cellulose reaction. This is in marked contrast to *R. agile*, whose sporangial walls Zopf describes as being composed of cellulose.

The zoospores, figure 26, are hyaline, spherical,  $2.5-3\ \mu$  in diameter with a small refractive globule usually lying in the posterior region. The cilium is approximately  $25\ \mu$  in length. The swarmspores dart about with great rapidity, and may remain actively motile for more than half an hour. They may occasionally become amoeboid, figure 25, but this is not nearly as marked as in *R. sphaerocarpum*. Germination occurs quite frequently in water, figures 27-29, and often more than one germ tube may develop. During germination the zoospore becomes vacuolated, and the refractive globule is thus displaced towards the periphery, figure 29.

[The further development of the thallus is fundamentally similar to that of other species of *Rhizophidium*. After the germ tube has branched to form the rudiments of the rhizoidal system, and the latter has become somewhat extended, the zoospore begins to enlarge into an incipient sporangium. Figure 30 shows a very early stage in which the young spo-

#### Explanation of Plate 20

##### *Rhizophidium macrosporum* n. sp.

Fig. 1. A large thallus from cooked beef with an extended rhizoidal system and a spherical zoosporangium filled with large refractive globules.

Fig. 2. Smaller urn-shaped sporangium with three exit papillae and two main rhizoidal axes.

Fig. 3. A stalked sporangium with four exit papillae.

Fig. 4. A small sporangium with three separated rhizoidal axes.

Fig. 5. A zoospore showing the unusually large refractive globule.

Figs. 6-8. Amoeboid zoospores showing the changes in shape undergone by the refractive globule during amoeboid movement.

Fig. 9. A quiescent, greatly expanded zoospore which failed to emerge from the sporangium.

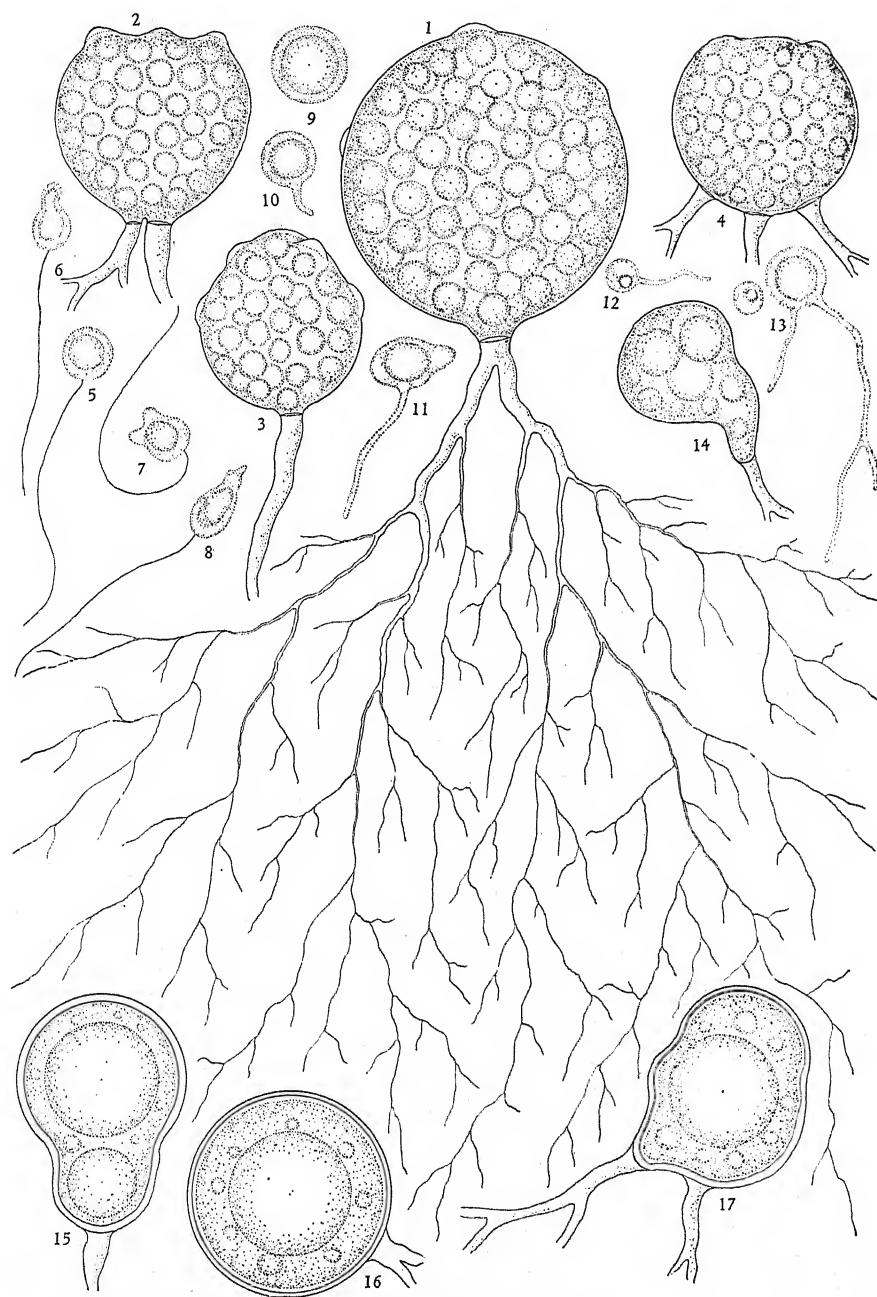
Figs. 10, 11. Early germination stages.

Fig. 12. Germination of a zoospore of *Rhizophidium* sp., with the germ tube directed towards a swarmspore of *R. macrosporum*.

Fig. 13. A zoospore of *Rhizophidium* sp. lying close to a germinating swarmspore of *R. macrosporum*.

Fig. 14. An early stage of resting spore development.

Figs. 15-17. Variations in the size and shape of the resting spores.



KARLING: RHIZOPHIDIUM

rangium is quite vacuolated. This condition appears to be characteristic of the early developmental stages, as Couch (figs. 54, 55) has shown for *P. bisporum* also. Furthermore, the remainder of the protoplasm is rather pearly opaque and not as refringent as I have observed it in other species. In figure 31 is shown a half grown sporangium with three conspicuous vacuoles. One of them contains a dark globule which showed striking Brownian movement. This sporangium was kept under observation for a long time, and during this period the three vacuoles were continually changing in shape and position, indicating a definite circulation or movement of the protoplasm. Eventually these vacuoles fused into a large central one, as is illustrated in the sporangium of figure 32. As the sporangia increase in size and mature the vacuolate condition gradually disappears. The movement and fusion of the vacuoles described above are the only unusual characteristics I have observed in the development of the sporangia.

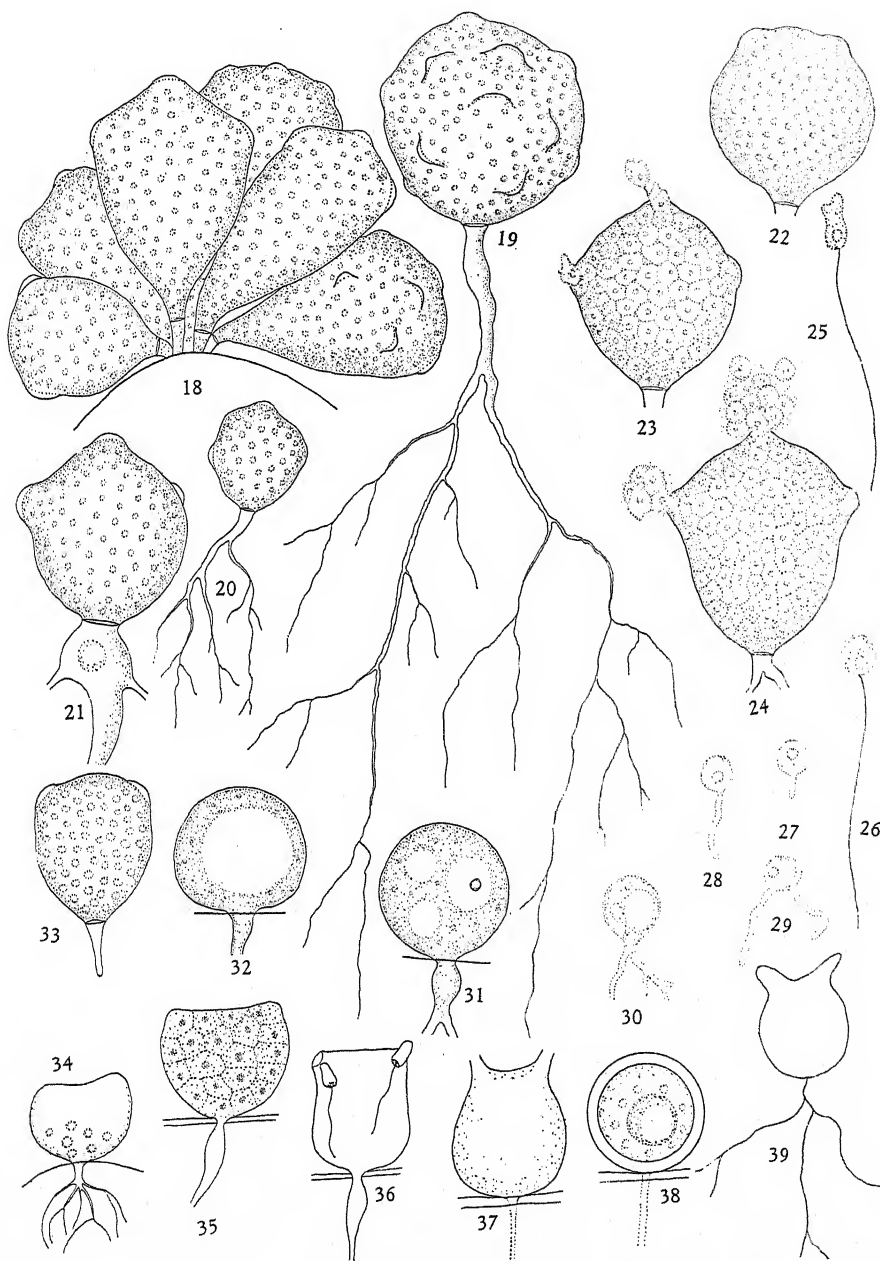
As has been stated above no resting spores were found on any of the host material employed. In two instances a light brown, thick-walled, spherical,  $9\ \mu$  resting spore with a large,  $5\ \mu$  refringent globule in the center and a long hyaline, attached, haustorium-like peg was observed, but I am not certain that it relates to our species. It is to be noted in this connection that Zopf and Couch also failed to find the resting spores of *R. agile*, *R. gibbosum* and *P. bisporum* in spite of repeated search over a long period of

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#### Explanation of Plate 21

##### *Rhizophidium* sp.

- Fig. 18. A group of stalked, somewhat triangular-shaped sporangia on the surface of a liver fluke ovum.
- Fig. 19. A large thallus on the ovarian tissue of *Hepatica fasciola*.
- Fig. 20. A minute thallus drawn for comparison with the one shown in fig. 19.
- Fig. 21. A portion of a thallus from root tips of *Narcissus* showing the inflated, apophysis-like rhizoidal stalk.
- Fig. 22. A sporangium with two exit papillae shortly before cleavage.
- Fig. 23. An initial stage in the emergence of the zoospores.
- Fig. 24. Emergence of the zoospores from a large sporangium.
- Fig. 25. An amoeboid zoospore.
- Fig. 26. A zoospore during the active swimming stage.
- Figs. 27-29. Germination stages.
- Figs. 30-32. Stages in the development of the zoosporangium.
- Fig. 33. A small free-floating sporangium with two exit papillae.
- Fig. 34. A small sporangium of *R. agile* after Zopf.
- Figs. 35, 36. Sporangia of *Phlyctochytrium bisporum* after Couch.
- Figs. 37, 38. A sporangium and resting spore of *P. bisporum* after Sparrow.
- Fig. 39. A thallus of *R. rostellatum* after de Wildeman.



KARLING: RHIZOPHIDIUM



time. Whether or not this may indicate a possible relationship or identity of these species with ours is of course a matter of speculation.

#### DISCUSSION

As has been noted above the small sporangia of *Rhizophidium* sp. frequently bears considerable resemblance to those of *R. agile*, *R. gibbosum*, *R. rotellatum*, and *Phlyctochytrium bisporum*. With the view of presenting these similarities more concisely I have brought together in figures 34 to 39 thalli of these species as they have been illustrated by Zopf, Couch, Sparrow and de Wildeman. This is, of course, a selected group of drawings and shows only the thalli which are similar as to shape. *Rhizophidium agile* was described by Zopf (1888) and Serbinow (1907) on *Chroococcus turgida*, and is characterized by small, 10–15  $\mu$ , slightly triangular sporangia with an apical exit papilla, minute, 2.5  $\mu$ , zoospores, and a virulently parasitic nature. The smallest sporangia of our species fall within the size magnitude of those of *R. agile*, but the largest ones may be five times as great in diameter. Furthermore, as many as 11 exit papillae may occasionally be present on such sporangia, giving them a distinct gibbose appearance. In this respect they may frequently resemble some of the sporangia of *R. gibbosum* Zopf (1888) on species of *Cylindrocystis*, *Phycastrum* and *Penium*. The zoospores of *R. gibbosum* are similar to those of our species in size, behavior, and general appearance, but the sporangia have only a single functional apical papilla, according to Zopf.

The sporangia, zoospores and rhizoidal system of our species are also often very similar to those of *Phlyctochytrium bisporum* described by Couch (1932) and Sparrow (1933, 1936) on *Vaucheria*, *Oedogonium*, *Bumilleria* and *Spirogyra*. This species is characterized by small, 8–13  $\mu$ , sporangia with two exit papillae or orifices near the apex which give them a somewhat triangular shape, figures 35–37, an occasionally inflated rhizoidal stalk, and zoospores which measure 2.6–3  $\mu$  in diameter. A comparison of Couch's and Sparrow's drawings with my figures 18, 22, 23, 24 and 33 show a striking similarity in shape relative to the smaller sporangia. A further similarity is suggested by Couch's report that his species usually grows on the disorganized cells of the host, which indicates that it may be largely saprophytic. Couch failed to observe the resting spores, but Sparrow (1936) found hyaline, spherical, thick-walled spores, figure 38, associated with the sporangia which he believes may belong to *P. bisporum*. He further believes that Couch's species is the same as *R. rotellatum* (de Wildeman) Fischer which occurs on *Spirogyra crassa*. Figure 39 shows a thallus of the latter species as drawn by de Wildeman and in the presence of the two horn-like exit papillae it is very similar to Sparrow's drawing, figure 37, of *P. bisporum*.



The occasional similarities in size and shape of the sporangia and zoospores of our chytrid with those listed above may indicate a close relationship of these species, but until more is known about them, it is impossible to determine whether or not they are identical. Characters such as size and appearance of sporangia, number of exit papillae, etc., are often highly variable and, within certain limits, of doubtful diagnostic value, so that too much significance must not be attached to them. Accordingly, in view of the fact that I have so far failed to find the resting spores in *Rhizophidium* sp., I shall for the time being leave it unidentified. I am none the less continuing my study on it with the hopes of observing its complete life cycle.

The present study shows how ubiquitous and large species of *Rhizophidium* may be. The majority of species are described in the literature as being comparatively small and parasitic or weakly saprophytic. *Rhizophidium macrosporum* and *Rhizophidium* sp., appear at present to be primarily saprophytic and capable of growing on a wide variety of dead animal and plant tissues. Furthermore, in the former species the thalli may attain the size of species of *Entophlyctis*, *Endochytrium*, *Diplophlyctis*, etc. Doubtless as more intensive studies of individual species are made, we shall find an even greater variability in size and host range.

#### SUMMARY

*Rhizophidium macrosporum* was first observed on cooked ground beef, and has subsequently been grown on various sterilized filamentous algae and root tips. It is characterized by large spherical (22–110  $\mu$ ) oval and broadly pyriform, hyaline, smooth sporangia, spherical (4.5–6  $\mu$ ) zoospores with an unusually large refractive globule, a coarse extensive rhizoidal system, and large spherical (15–30  $\mu$ ) or oval (18 $\times$ 20–22 $\times$ 37  $\mu$ ) hyaline resting spores.

*Rhizophidium* sp. occurs saprophytically on a wide variety of dead filamentous and unicellular algae, flagellates, rhizopods, rotifers, liver fluke ova and ovarian tissue, eggs, larvae and exuviae of insects, cooked striated muscle cells and root tips of various plants. The sporangia may be almost spherical (10–52  $\mu$ ), slightly depressed, wedge-shaped and somewhat triangular (14 $\times$ 29  $\mu$ –25 $\times$ 30  $\mu$ ) oval and occasionally slightly irregular with 1 to 11 exit papillae. The smaller sporangia may often resemble those of *R. agile*, *R. gibbosum*, *R. rostellatum* and *Phlyctochytrium bisporum*. Resting spores have so far not been found.

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## Thiamin and growth of *Pythium Butleri*

WILLIAM J. ROBBINS AND FREDERICK KAVANAGH  
(WITH THREE FIGURES)

Studies on the relation of thiamin (vitamin B<sub>1</sub>) to the growth of fungi have shown that on the basis of our present knowledge they may be arranged in at least three groups.

GROUP I includes those which synthesize thiamin from the elementary materials of the medium and require for growth no external supply of thiamin or its intermediates. The growth of some of these plants is not materially affected by the addition of thiamin to the medium; that of others is inhibited by its addition (3).

GROUP II includes those which do not synthesize thiamin or its intermediates from the constituents of the medium. Some of these are incapable of forming thiamin from the thiazole and pyrimidine intermediates; for growth to occur they require an external supply of the vitamin as such (4, 5). Others are capable of forming the vitamin from the intermediate thiazole and pyrimidine, but are incapable of synthesizing the intermediates themselves. These plants require for growth an external supply of thiamin or of both intermediates (2, 7, 8, 9).

GROUP III includes those which do not synthesize thiamin but are able to form one or the other of the vitamin intermediates. Some form pyrimidine; these grow if furnished with thiamin or with the vitamin thiazole (1); others form thiazole and grow if supplied with thiamin or the vitamin pyrimidine (3, 10).

*Pythium Butleri* Subramanian differs somewhat from all the types described above. Under certain conditions this organism appears to form thiamin but in amounts inadequate for maximum growth; under other conditions it forms little or no thiamin. In either instance the addition of thiamin or of pyrimidine increases the rate of growth. In its ability to grow in media containing no growth supplement it resembles the organisms of GROUP I; in its response to thiamin and pyrimidine, the organisms of GROUP III.

### METHODS AND MATERIALS

The culture of *Pythium Butleri* was furnished by J. T. Middleton. Stock cultures were maintained on potato dextrose agar.

Several nutrient solutions were used as follows:

SOLUTION D, containing about 16.4 g. of salts per liter, was composed of MgSO<sub>4</sub>·7H<sub>2</sub>O, 5.0 g.; KH<sub>2</sub>PO<sub>4</sub>, 10.32 g.; Na<sub>2</sub>HPO<sub>4</sub>, 0.575 g.; NH<sub>4</sub>NO<sub>3</sub>, 0.5.; asparagine, 5.0 g.: dextrose (cerelose), 50.0 g. and redistilled water, 1000 cc. To each liter of the above solution 1 ml. of a modified Hoagland's

A to Z mixture (3) was added. The hydron concentration was pH 5.5.

SOLUTION E, containing about 1.64 g. of salts per liter, was made by diluting the salts and asparagine of solution D ten times and reducing the dextrose to 20 g. per liter.

SOLUTION G, containing about 1.64 g. of salts per liter, was made by diluting the salts of solution D ten times but maintaining the asparagine and dextrose concentrations unchanged.

SOLUTION I contained no organic nitrogen. It was composed of  $\text{MgSO}_4 \cdot 7\text{H}_2\text{O}$ , 0.25 g.;  $\text{KH}_2\text{PO}_4$ , 0.5 g.;  $\text{NH}_4\text{NO}_3$ , 1.0 g.;  $\text{KNO}_3$ , 1.0 g.; dextrose, 25.0 g. and redistilled water 1000 cc. To each liter of this solution 1 ml. of a mixture of Steinberg's mineral supplements (4) was added.

The thiamin chloride used was a crystalline product (betabion) from Merck and Co. The thiamin intermediates, supplied through the courtesy of Merck and Co., were 2-methyl-5-bromomethyl-6-amino pyrimidine hydrobromide, 2 methyl-5-ethoxymethyl-6-amino pyrimidine, and 4-methyl-5 $\beta$ -hydroxyethyl thiazole. For brevity the first mentioned pyrimidine and the thiazole are referred to in this paper as pyrimidine and thiazole respectively.

The asparagine was repurified by solution in water and precipitation with alcohol for all experiments except those with solution D. The dextrose was a sample of high purity (cerelose) from the Corn Products Co.

The solutions were sterilized at 12 lbs. pressure for 20 minutes. In some instances the thiamin was filtered sterile and added to the basic nutrient solutions which had been sterilized by heating.

The *Pythium* was grown at room temperature (20–25°C) in 25 ml. of solution in 125 ml. flasks of pyrex glass. The solution in the flask was inoculated by transferring a bit of mycelium from the stock cultures. In making inoculations care was used to avoid transferring any of the medium in which the inoculum had grown. All cultures were grown in triplicate.

Dry weights were determined by washing the mycelium with water to remove the sugar and drying at 100°C. Some difficulty was experienced in washing the mycelium free of sugar, and the dry weights in the earlier experiments were influenced to some extent by residual sugar.

#### EXPERIMENTAL

SOLUTION D.—*P. Butleri* grew very poorly in solution D forming but 4 mg. of dry mycelium in 19 days. The addition of 3 units<sup>1</sup> or 30 units of thiamin increased the growth more than 70 times (table 1). The addition of thiazole alone had little effect but pyrimidine alone was quite effective. A mixture of thiazole and pyrimidine increased growth but much less

<sup>1</sup> A unit is  $10^{-9}$  Mole of the compound.

than molecularly equivalent amounts of thiamin. The effects of supplementing solution D with thiamin or its intermediates on the growth of *P. Butleri* are shown in figure 1.

We are uncertain as to how much reliance should be placed on the differences in dry weights in the solutions supplemented with thiamin, pyrimidine and the mixtures of thiazole and pyrimidine. It would seem from the photographs taken at the end of 14 days incubation (fig. 1) and the dry weights determined after 19 days growth (table 1) that thiamin

TABLE 1

*Dry weight of mycelium of Pythium Butleri grown 19 days in solution D, 14 days in solution G or 19 days in solution I and in the same solutions supplemented with thiamin or its intermediates*

SUPPLEMENT	DRY WT. MG. MYCELIUM SOLUTION D	DRY WT. MG. MYCELIUM SOLUTION G	SUPPLEMENT	DRY WT. MG. MYCELIUM SOLUTION I
None	4	149 ± 21	None	39 ± 4
3 units thiamin	285 ± 15	168 ± 10	5 units thiamin	110 ± 4
30 units thiamin	305 ± 5	210 ± 3	5 units thiazole	73 ± 9
3 units thiazole	13	169	5 units pyrimidine	103 ± 3
30 units thiazole	26 ± 33	180 ± 4	5 units thiazole and 5 units pyrimidine	94 ± 9
3 units pyrimidine	249 ± 32	236 ± 11	dextrose only no salts	0.6
30 units pyrimidine	230 ± 25	293 ± 7		
3 units thiazole and 3 units pyrimidine	23	266 ± 27		
30 units thiazole and 30 units pyrimidine	135 ± 15	305 ± 10		

was more effective in solution D than either pyrimidine alone or the mixture of thiazole and pyrimidine. It would appear also that the mixture of thiazole and pyrimidine was less effective than molecularly equivalent quantities of pyrimidine. Before such conclusions can be drawn additional experiments with solution D should be performed; uniformity in inoculations with this organism is difficult to secure. Furthermore, the time factor is important as may be noted by comparing the relative growth of the fungus in the solutions supplemented with thiamin and its intermediates as shown in the photograph taken after 14 days growth and the relative dry weights formed at the end of 19 days. In any event the beneficial



effect of the additions of thiamin and of pyrimidine to the medium were clear.

During the course of this experiment the growth in one of the flasks supplemented with 3 units of pyrimidine was observed to be considerably heavier than that in the other two. Microscopic examination showed contamination by a rod shaped bacterium in this flask. It is probable that thiamin formed by the contaminating organism was responsible for the more rapid growth of *Pythium* in the contaminated culture (fig. 2).

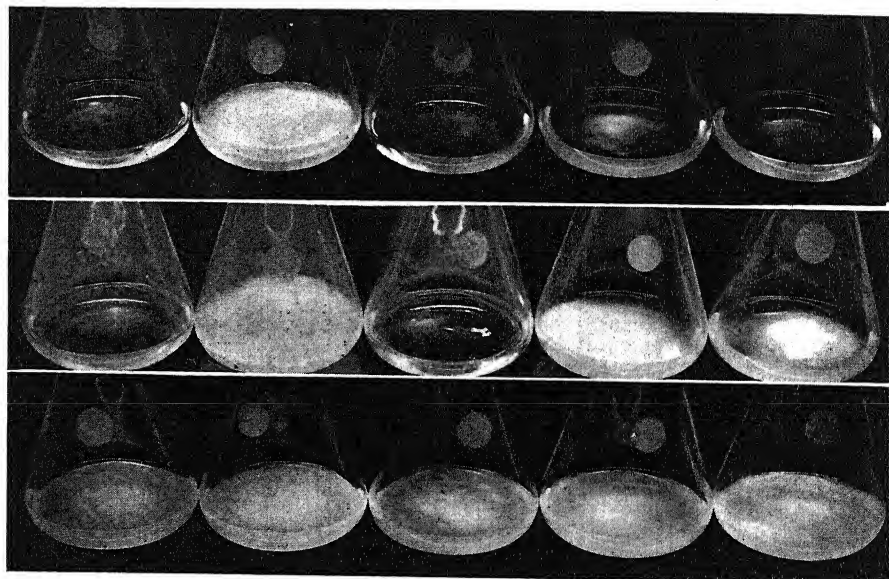


Fig. 1. Growth of *Pythium Butleri* in solutions supplemented with thiamin or its intermediates. Above, solution D with 3 units of supplements; center, solution D with 30 units of supplements; below, solution E with 30 units of supplements. In each series from left to right; no supplement, thiamin, thiazole, pyrimidine, thiazole and pyrimidine. Period of growth 14 days.

It would seem from the results with solution D that *P. Butleri* belongs with those organisms described above in GROUP III which grew satisfactorily with the addition to the basic medium of either thiamin or the intermediate pyrimidine. However, when solution D was diluted differences in the response of this fungus and those mentioned earlier became apparent.

SOLUTION E.—*P. Butleri* grew in solution E without the addition of any supplement (fig. 1). In 19 days it formed 45 mg. of dry mycelium under the same conditions in which it formed but 4 mg. in solution D. To eliminate the possibility that this growth was made at the expense of



thiamin carried over in the inoculum a subculture was made from the growth in solution E to a fresh lot of the same solution. In 19 days mycelium of 68 mg. dry weight was produced. A third transfer yielded 76 mg. in 14 days. *P. Butleri* appeared to be capable of growing indefinitely in a suitable solution to which no supplement had been added.

The addition of 3 units or of 30 units of thiamin to solution E increased the growth, the effect showing more sharply in the early stages of development than later. However, much less mycelium developed in solution E in the presence of thiamin than in solution D, which was taken to indicate that some factor (probably the nitrogen content) limited growth in the former medium. To obviate this difficulty solution G was used.

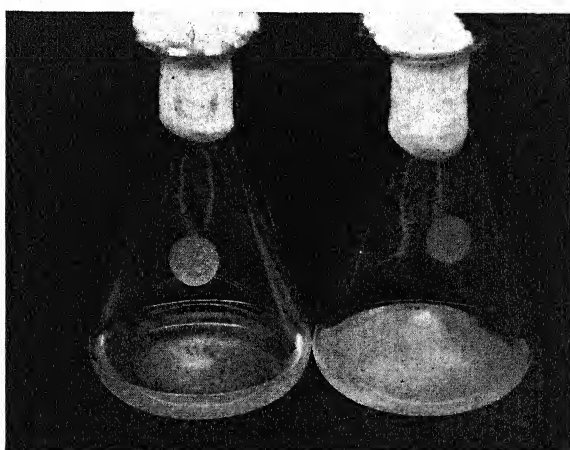


Fig. 2. Effect of contaminating bacteria on growth of *P. Butleri* in solution D plus 3 units pyrimidine. Left, uncontaminated; right, contaminated. Period of growth 14 days.

**SOLUTION G.**—In this solution (table 1) *P. Butleri* formed 149 mg. of dry mycelium in 14 days. The addition to solution G of thiamin, of pyrimidine, or of the mixture of thiazole and pyrimidine increased the growth. Thiazole alone had little effect. From three to four times as much mycelium was formed in solution G as was produced in the same time in solution E. This was interpreted to be the result of the greater amount of asparagine and dextrose furnished in solution G.

Solutions D, E, and G contained asparagine which is an organic substance of natural origin. In order to eliminate the asparagine as a complicating factor a solution was used containing no nitrogen other than inorganic nitrogen.

**SOLUTION I.**—*P. Butleri* grew slowly in solution I forming a mycelium

of 39 mg. in 19 days. A subculture from this solution to more of the same medium yielded 120 mg. in 26 days; a third, fourth and fifth successive transfer to solution I was made with no evident diminution in the rate

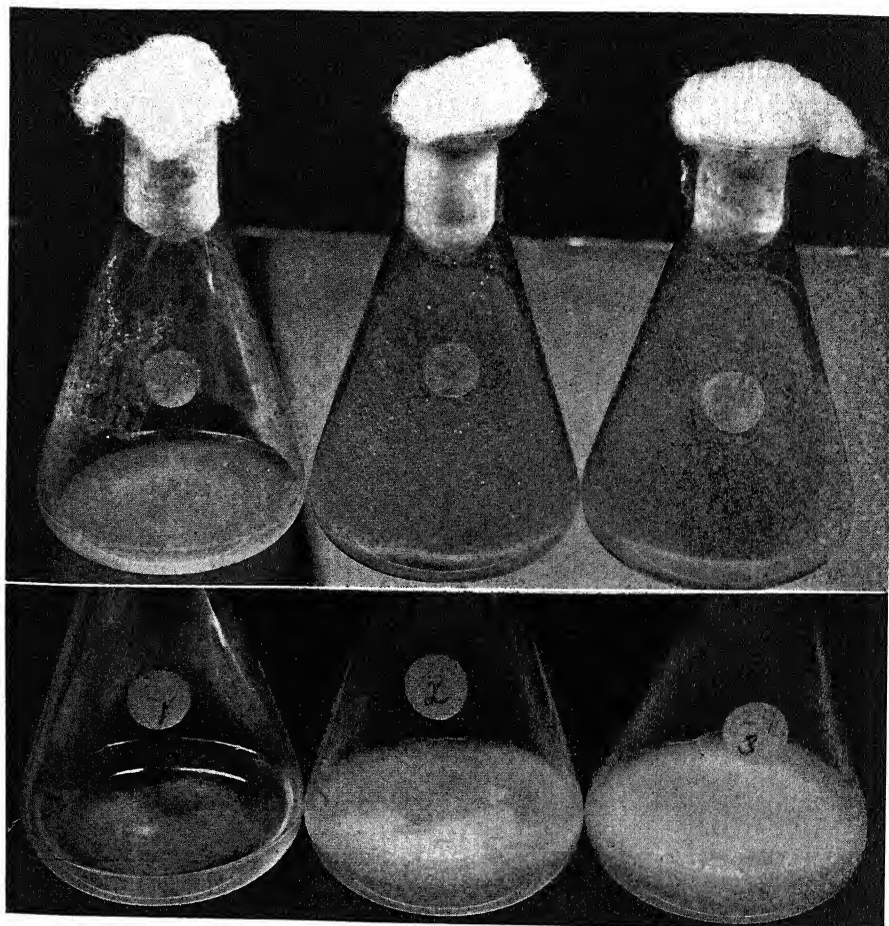


Fig. 3. Formation of thiazole by *P. Butleri*. Below from left to right, solution D plus thiazole, plus pyrimidine, plus thiazole and pyrimidine. Above, same solutions sterilized, mycelium removed and inoculated with *Phycomyces Blakesleeanus*.

of growth. These results indicate that this fungus is capable of unlimited growth in a mineral solution containing dextrose.

The addition of thiamin, of ethoxypyrimidine or of thiazole and pyrimidine to solution I increased the growth of *P. Butleri* (table 1), each of the compounds or combination of compounds being nearly equally effective. Thiazole produced a small increase.

*Formation of thiamin and intermediates by P. Butleri.*—The results

given above show that the growth of *P. Butleri* in the solutions used was improved by the addition of thiamin or of pyrimidine. The effect of thiazole was less marked. How should these results be interpreted? Does the fungus require thiamin forming some, though insufficient for maximum growth, in the unsupplemented solutions and synthesizing thiazole in the solutions supplemented with pyrimidine? Or does it require pyrimidine only, synthesizing small quantities in the unsupplemented solutions and securing the necessary amount in the thiamin cultures by splitting the vitamin into its thiazole and pyrimidine constituents? We have no direct evidence to show the need for thiamin as such, though we are inclined to believe that the organism requires the vitamin rather than the intermediates. We have evidence, however, that in the thiazole solutions *P. Butleri* forms some pyrimidine and in the pyrimidine cultures it forms considerable thiazole. In other words, *P. Butleri* requires both intermediates for growth forming thiazole more readily than pyrimidine. The evidence upon which this conclusion is based is as follows:

*P. Butleri* was grown in solution D supplemented with 30 units of thiazole, 30 units of pyrimidine or 30 units of both intermediates. The growth in the thiazole solutions was slight; it was considerably heavier in the solutions containing pyrimidine or both intermediates (see fig. 3). At the end of 19 days the mycelium of *P. Butleri* was removed, the solutions sterilized and inoculated with *Phycomyces Blakesleeanus*. This fungus has been demonstrated to require for growth an external supply of thiamin or of both intermediates. At the end of twelve days *Phycomyces* had produced some submersed mycelium in the solution originally supplemented with thiazole only, indicating the formation of a small quantity of pyrimidine. In the solution originally supplemented with pyrimidine only there was a heavy development of aerial mycelium with sporangia and sporangiophores showing the formation of 3 units of thiazole or more. These results indicate that *P. Butleri* requires both intermediates for growth and synthesizes more thiazole than pyrimidine.

#### DISCUSSION

We have interpreted the results of the experiments described above to mean that *P. Butleri* requires thiamin for growth, in the more dilute solutions used (solutions E, G and I) the fungus synthesized from the more elementary constituents of the medium sufficient vitamin for slow growth but insufficient for maximum growth. In other words, in these solutions the amount of thiamin formed by the organism was the factor limiting growth. Judging from the effect when pyrimidine alone was used as a supplement it would seem that a slow formation by the organism of

the pyrimidine portion of the vitamin molecule was the limiting factor in solutions E, G, and I.

On the basis of the above interpretation we would explain the failure of *P. Butleri* to grow in solution D as follows: In this solution the total salt concentration or concentration of some particular salt interfered with the synthesis of thiamin. The assumption that the salt concentration interfered with thiamin synthesis rather than the functioning of the vitamin would seem to follow since the addition of thiamin to solution D markedly improved the growth; it was effective if present. We cannot say definitely whether the salt concentration interfered with the synthesis of the intermediates by *P. Butleri* or the synthesis of thiamin from the intermediates. The latter would be suggested by the relatively poorer growth in the solution D supplemented with thiazole and pyrimidine than in the same solution supplemented with thiamin. This difference did not appear in the more dilute solutions (solutions G and I, table 1). However, the salt concentration appeared to interfere with the formation of the pyrimidine portion of the vitamin more than it did with the thiazole portion. This follows because growth in solution D supplemented with thiazole alone was much less, relative to that in the same solution supplemented with thiamin or with pyrimidine, than in the more dilute solution G (table 1).

The beneficial effect on the growth of *P. Butleri* of the dilution of solution D and of the addition of thiamin to the same solution is similar to the results reported by Seager (6) for *Lemna*. Seager observed that *Lemna* did not grow indefinitely in Knop's solution. The addition of dried yeast to Knop's solution or the dilution of the solution to 1/10 its normal strength permitted growth to occur, although even in the dilute Knop's solution the addition of yeast was beneficial.

The response of *P. Butleri* to thiamin and its intermediates is of particular interest because it shows that salt concentrations may injure a plant because of its effect upon thiamin production. Why should this be true of *P. Butleri* and not of *Aspergillus niger* which grows well in solution D? Furthermore, other organisms which have been reported incapable of synthesizing thiamin should be tested in various solutions and conditions since the formation of thiamin by *P. Butleri* was influenced by the conditions (mineral salt concentration) of culture.

#### SUMMARY

The growth of *Pythium Butleri* in a mineral salt solution containing asparagine and sugar (solution D) was negligible. The addition of thiamin or the vitamin pyrimidine markedly increased the growth.

*P. Butleri* was capable of unlimited growth when the salts of solution D were diluted; growth was increased in this solution by the addition of thiamin or pyrimidine.

Contaminating bacteria in one instance increased growth of *P. Butleri*.

The formation of thiazole and of smaller amounts of pyrimidine was demonstrated.

It is concluded that under the conditions of these experiments the growth of *P. Butleri* was limited by its thiamin production which was affected by the concentration of salts in the solution.

THE NEW YORK BOTANICAL GARDEN

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## Studies in the American Celastraceae I. New species of *Microtropis*, *Wimmeria* and *Zinowiewia*<sup>1</sup>

C. L. LUNDELL  
(WITH THREE FIGURES)

In studies of the Mexican and Central American flora, particularly that of the Maya area, the need for a systematic study of the Celastraceae has interested the writer. Through a preliminary series of revisions of the genera of American Celastraceae, it is hoped that interest of collectors will be stimulated so that material of many of the lesser known genera and species can be accumulated to make possible later an adequate monographic treatment of the family. As illustrated by the situation in the genus *Zinowiewia*, many of the celastraceous species are poorly represented in herbaria, all too many being known from a single collection. That many interesting forms remain to be discovered is evident; no less than four of the new species of *Zinowiewia* were collected for the first time between 1933 and 1937.

Included in this paper are nine new species which represent undescribed forms discovered in revising the American species of *Microtropis*, and the genera *Wimmeria* and *Zinowiewia*.

In the list of citations of herbarium specimens, the following abbreviations of the names of herbaria are employed:

- A—Arnold Arboretum, Jamaica Plain, Mass.
- D—Dudley Herbarium, Stanford University, Calif.
- F—Field Museum of Natural History, Chicago, Ill.
- G—Gray Herbarium, Harvard University, Cambridge, Mass.
- K—Royal Botanic Gardens, Kew, Surrey, England
- M—University of Michigan, Ann Arbor, Mich.
- Mo—Missouri Botanical Garden, St. Louis, Mo.
- NY—New York Botanical Garden, New York, N. Y.
- P—Academy of Natural Sciences, Philadelphia, Pa.
- US—United States National Herbarium, Washington, D. C.

The writer is deeply indebted to the directors and curators of these institutions for their courtesy in making the material available. All of the cited specimens have been uniformly annotated with printed labels.

***Microtropis Standleyi* sp. nov.**—Frutex epiphyticus, 2-metralis. Folia 5–8 mm. longe petiolata, chartacea, discolora, lanceolato-elliptica vel oblongo-elliptica, 5.5–9.5 cm. longa, 1.8–3.8 cm. lata, apice breviter acuminata, acumine obtusiusculo, basi cuneata vel acutiuscula. Cymae 2.3 cm. longae vel minores. Flores masculi virides. Sepala inaequalia, suborbicularia vel late

<sup>1</sup> Papers from the Herbarium of the University of Michigan.

ovato-orbicularia, 2 exteriora 1.2–1.4 mm. lata, interiora 1.5–2.2 mm. lata, margine minute erosa. Petala late obovata vel suborbicularia, 2–2.4 mm. longa, margine minute erosa. Discus pentagonus, crassus, ca. 1.8 mm. diam. Filamenta ca. 1 mm. longa. Antherae late cordatae, ca. 0.5 mm. longae. Ovarium in discum subimmersum. Flores femineos non vidi. Fructus ignotus.

An epiphytic shrub about 2 m. high, not scandent; branchlets usually opposite, rather slender, striate, drying reddish-black. Leaves chartaceous, paler beneath, margin entire, slightly revolute. Petioles canaliculate, 5 to 8 mm. long. Leaf blades lanceolate-elliptic or oblong-elliptic, 5.5 to 9.5 cm. long, 1.8 to 3.8 cm. wide, apex short acuminate, the acumen obtusish, base cuneate or acutish, costa prominent beneath, prominulous above, main lateral veins 4 or 5 on each side, strongly ascending from base, arcuately ascending from medial region, prominulous beneath, fainter above, veinlets inconspicuous. Cymes 2.3 cm. long or less, divaricately forked 3 to 5 times, each node bibracteate; peduncles stout, 3.5 to 7.5 mm. long; primary branches 2 to 4 mm. long; ultimate branches shorter. Bracts and bractlets semicymbiform, 1 to 1.5 mm. long, margin minutely erose, reddish. Staminate flowers green or pale green, pentamerous or tetramerous (excepting ovary), subsessile or with a very short thick pedicel. Sepals strongly unequal, suborbicular or broadly ovate-orbicular, the 2 outer 1.2 to 1.4 mm. wide, the inner 1.5 to 2.2 mm. wide, margin obscurely and minutely erose, reddish. Petals broadly obovate or suborbicular, 2 to 2.4 mm. long, margin very minutely erose. Disk usually pentagonous, rather thick, about 1.8 mm. wide, subcupular. Filaments inserted on angles of disk, about 1 mm. long; anthers broadly cordate, about 0.5 mm. long, short apiculate. Rudimentary ovary almost entirely submerged in disk, contracted above into a short style, incompletely 2-celled, with 4 collateral ovules on a short central placenta. Pistillate flowers and fruits unknown.

Type in the Herbarium of the Field Museum of Natural History (No. 599,103), *P. C. Standley and Juvenal Valerio 50602*, collected on Cerros de Zurquí, northeast of San Isidro, Province of Heredia, COSTA RICA, alt. 2000–2400 m., Mar. 3, 1926.

Additional specimens examined: COSTA RICA: Province of Heredia, Cerros de Zurquí, northeast of San Isidro, alt. 2000–2400 m., Mar. 3, 1926, *Standley and Valerio 50602*, staminate flowers, type collection (US); *Standley and Valerio 50480*, staminate flowers (F, US). Province of San José, Zurquí, alt. 2000–2500 m.; shrub in wet forest; Feb. 13, 1926, *Standley and Valerio 48169*, staminate flowers (US).

*M. Standleyi* is related to *M. Schiedeana* Loes. of Vera Cruz, but may be readily distinguished by its chartaceous leaves with main lateral veins 4 or 5 on each side, these strongly ascending from base at an acute angle, arcuately ascending from medial region. In *M. Schiedeana* the leaves are

subcoriaceous with main lateral veins 7 to 9 on each side, these patent, nearly horizontal.

*Wimmeria acapulcensis* sp. nov. (fig. 1).—Frutex. Folia 5–15 mm. longe petiolata, subcoriacea, remotè et inconspicue serrulata, lanceolata vel ovata, 4.5–7 cm. longa, 2–3.8 cm. lata, apice obtusa vel rotundata, basi attenuata, acuminata, costa ad apicem utrinque debili, venis supra albidis, inconspicuis, subtus leviter impressis, obscuris. Cymae minute puberulae, longe pedunculatae. Pedicelli 5–6 mm. longi, ad basin puberuli. Calycis lobi inaequales, 1.4–2.5 mm. lati. Petala 5, minute pulverulento-puberula, suborbicularia, ca. 3 mm. longa secus medietatem, marginibus ca. 0.8 mm. ultra apicem productis. Filamenta ca. 2.3 mm. longa. Ovarium 3- raro 2-loculare, stylo crasso, ca. 0.8 mm. longo. Fructus depresso-orbiculares, 13–18 mm. longi, 18–22.5 mm. lati.

"A spreading shrub 24 dm. high" (Rose); branchlets pale, rather stout, compressed and strongly striate, puberulent around the nodes, glabrous otherwise. Leaves subcoriaceous, brittle, slightly paler beneath, borne mainly on short spur-like branches. Stipules minute. Petioles 5 to 15 mm. long, slender, shallowly canaliculate, puberulent above, the medial ridge conspicuous. Leaf blades lanceolate or ovate, 4.5 to 7 cm. long, 2 to 3.8 cm. wide, apex bluntly obtuse to rounded, base attenuate, acuminate, decurrent, costa prominent at base beneath, less conspicuous above, becoming faint near the apex, veins nearly plane above, whitened, impressed and almost obsolete beneath, margin remotely and inconspicuously serrulate with minute appressed nigrescent teeth. Cymes puberulent, long pedunculate, forked 1 to 3 times, the ultimate branches shortened, crowding the flowers. Bracts and bractlets minute, with toothed margins, the teeth red. Pedicels slender, puberulent only at base, 5 to 6 mm. long, jointed at base. Calyx 5-lobed, the lobes unequal, broadly rounded, 1.4 to 2.5 mm. wide, minutely apiculate, very minutely erose-ciliolate. Petals 5, minutely pulverulent-puberulent outside, 7- or 8-veined, suborbicular, 3 mm. long medially, with the overlapped margin prolonged laterally at apex as much as 0.8 mm., about 3.2 mm. wide, rufous-punctate, free margin very minutely ciliolate, overlapped margin erose. Stamens 5; filaments filiform-subulate, about 2.3 mm. long, inserted on lower edge of disk; anthers 1 mm. long. Disk thick, nearly flat, confluent with base of ovary, slightly rugose, minutely papillate. Ovary 3-winged, rarely 2-winged, 3-celled, rarely 2-celled, base submerged in disk. Style thick, terete, about 0.8 mm. long. Stigma subcapitate, trifid, rarely bifid. Fruits 3-winged, rarely 2-winged, usually broadest at the middle, depressed-orbicular, much wider than long, 13 to 18 mm. long, 18 to 22.5 mm. wide, crowned by the persistent stigma and style, deeply notched at apex and base, the wings membranous, with close veins; 1-seeded.

Type in the Herbarium of Arnold Arboretum, *Edward Palmer 124*, collected near Acapulco, Guerrero, Mexico, Nov. 1894.



Fig. 1. *Wimmeria acapulcensis* Lundell. Type collection (*Palmer 124*), in Missouri Botanical Garden Herbarium.  $\times \frac{1}{4}$

Additional specimens examined: MEXICO: Guerrero, Acapulco and vicinity, Nov. 1894, *Palmer 124*, type collection (G, Mo, US).

*Palmer 124* was described by Rose who made the untenable proposal to transfer the name *W. pallida* Radlk. to this species. (Contr. U. S. Nat. Herb. 5: 130. 1897.) *Hartweg 41* (fig. 2) is the type collection of *W. confusa* Hemsl., and *W. pallida* Radlk. (as to flowers). *W. confusa* has priority, hence *W. pallida* is clearly a synonym.

*W. acapulcensis* is very distinct from *W. confusa* (compare figs. 1 and 2), differing markedly in its much larger bluntly obtuse or rounded leaves and larger fruits. It is also related to *W. lanceolata* Rose and *W. persicifolia* Radlk. but may be readily distinguished as both of these have long attenuate-acuminate leaves.

***Wimmeria Bartlettii* sp. nov.**—Arbor glabra, 27 m. alta, 60 cm. diam. Folia 7–12 mm. longe petiolata, coriacea, lanceolata, lanceolato-oblonga vel elliptica, 6–13.5 cm. longa, 1.8–5.5 cm. lata, utrinque acuminata, serrulata. Cymae 1.3–3.5 cm. longae, pedunculatae. Pedicelli 3–13 mm. longi. Calyx profunde quinquefidus. Petala 5, late ovata, ca. 3 mm. longa in medietatem, marginibus lateralibus productis, fimbriatis, fimbriis saepe 1.3 mm. longis. Stamina 5. Filamenta 2.2–3 mm. longa. Antherae 1–1.2 mm. longae. Ovarium 3- raro 4-loculare. Fructus late ovati, suborbiculares vel oblongi, 3.5–5.2 cm. longi, 3–4 cm. lati.

A tree reaching a height of 27 m. and a diam. of 60 cm. (Bartlett, Lundell), with smooth gray bark; entirely glabrous; branchlets green, rather stout, striate. Leaves large, petiolate, coriaceous, slightly discolorous. Stipules minute, subulate, less than 1 mm. long. Petioles 7 to 12 mm. long, subcanaliculate above with a fine medial ridge. Leaf blades lanceolate, lanceolate-oblong, or elliptic, 6 to 13.5 cm. long, 1.8 to 5.5 cm. wide, acuminate at both ends, costa raised above as a narrow fine ridge extending nearly to apex, prominent beneath, main lateral veins 6 to 9 on each side, arcuately ascending, prominent to obscure on both surfaces, veinlets usually inconspicuous and obscure, rarely slightly impressed, margin serrulate, the teeth subulate-tipped with appressed nigrescent teeth. Cymes 1.3 to 3.5 cm. long, pedunculate, forked 2 to 4 times. Bracts and bractlets broadly triangular, acutish, 0.35 to 0.8 mm. long. Flowers green (Bartlett). Pedicels slender, 3 to 13 mm. long, jointed at base. Calyx rather thick, 5-lobed, the lobes imbricate, broadly ovate-triangular, rounded or bluntly obtuse. Corolla contorted, very rarely imbricate; petals 5, broadly ovate, about 3 mm. long medially, the overlapped margin prolonged laterally at apex, thin, conspicuously fringed, the fimbriae as much as 1.3 mm. long. Stamens 5; filaments filiform-subulate, 2.2 to 3 mm. long, inserted at edge of disk; anthers 1 to 1.2 mm. long. Disk large, rather flat, thick, rugose, shallowly 5-lobed, confluent with base of ovary, distinctly glandular-punctate. Ovary usually 3-angled, 3- rarely 4-celled, base submerged in disk. Style very short, usually triquetrous. Stigma trifid. Fruits crimson





Fig. 2. *Wimmeria confusa* Hemsl. Type collection (*Hartweg 41* from Zacatecas), in Kew Herbarium.  $\times \frac{3}{4}$ .



(Bartlett) or reddish-brown (Schipf), 3- rarely 4-winged, broadly ovate, broadly elliptic, or oblong in outline, 3.5 to 5.2 cm. long, 3 to 4 cm. wide at maturity, deeply cordate at base, shallowly emarginate to deeply notched at apex, crowned by the persistent stigma and style, the wings broad, membranous, with numerous fine close veins; 1- or 2-seeded, the seed erect, straight, linear, subterete, up to 1.8 cm. long, the testa finely verrucose, dark red; endosperm abundant; cotyledons flat, equal, linear-lanceolate, about 14 mm. long, apex obtuse; radicle up to 1.8 mm. long, subterete.

Type in the Herbarium of the University of Michigan, *H. H. Bartlett* 12435 (flowers), 12773 (fruits), collected in sapodilla and mahogany forest at Uaxactun, Department of Petén, Guatemala, April 2nd and 27th, 1931.

Additional specimens examined: GUATEMALA: Department of Petén, Uaxactun, in sapodilla and mahogany forest, March 21, 1931, *Bartlett* 12216, sterile (A, M); April 2, 1931, *Bartlett* 12435, type collection of flowers (A, Mo, NY, US); April 6, 1931, *Bartlett* 12481, flowers and fruits (A, D, M, NY, US); April 8, 1931, *Bartlett* 12536, flowers (A, M); April 27, 1931, *Bartlett* 12773, type collection of fruits (NY). La Libertad, Monte Chicbul, in forest on slope of limestone hill, *C. L. Lundell* 2640, sterile (M). Department of Izabal, lower Rio Dulce, March 2, 1885, *Sereno Watson* 43, fruits (G, K). BRITISH HONDURAS: El Cayo District, Valentin, in advanced, valley forest on limestone, June 27, 1936, *Lundell* 6278, flower buds (M-2). Toledo District, Temash River, on river bank in shade, April 22, 1934, *W. A. Schipp* 1296, fruits (A, F, G, M, Mo, NY).

Vernacular names: "Quiebra hacha blanco" (*Bartlett* 12216); "Chintoc" (*Bartlett* 12435); "Ixolte ixnuc" (*Bartlett* 12481).

Economic value: The wood is utilized locally for xylophone keys (*Bartlett*).

*W. Bartlettii* may be readily separated from the closely related *W. concolor* Schl. & Cham. by its much larger fruits as well as the fringed overlapped margin of the petals, the petals of *W. concolor* being merely erose on the overlapped margin.

*Zinowiewia australis* sp. nov.—Arbor 20 m. alta. Folia 6-8 mm. longe petiolata, subchartacea, ovato-elliptica, lanceolata vel elliptica, 5-8 cm. longa, 2.3-3.7 cm. lata, apice acuminata, acumine acutiusculo, basi abrupte attenuata, acuta. Fructus late oblanceolati vel obovati, 2-2.4 cm. longi, 7.5-9.5 mm. lati, apice rotundati, apiculati, valide venosi. Semen 1; cotyledonibus lanceolatis, 6.8-7.5 mm. longis, 2-2.1 mm. latis, apice rotundatis; radicula 3 mm. longa.

A tree about 20 m. high; branchlets slender. Leaves subchartaceous, dark green. Petioles slender, deeply canaliculate, 6 to 8 mm. long. Leaf blades

ovate-elliptic, lanceolate, or elliptic, 5 to 8 cm. long, 2.3 to 3.7 cm. wide, apex acuminate, the acumen acutish, base abruptly narrowed, acute, decurrent, costa slightly elevated above at base, prominent beneath, reticulate-veined, the main lateral veins 4 to 6, margin revolute. Cymes subsessile, forked 4 or 5 times, the primary branches much shortened. Fruits broadly oblanceolate to obovate, 2 to 2.4 cm. long, 7.5 to 9.5 mm. wide, strongly veined, the veins nearly horizontal above the middle, veinlets well-developed from margin of wing, apex rounded, apiculate; 1-seeded, the seed 9 to 11 mm. long, 2.5 to 3 mm. in diam., subterete, nearly straight, the ends narrowed, rounded; cotyledons lanceolate, 6.8 to 7.5 mm. long, 2 to 2.1 mm. wide, rounded at apex; radicle linear, quadrangulate, 3 mm. long.

Type in the Herbarium of the Field Museum of Natural History (No. 894,843), *H. Pittier 13826*, collected in "Selvas nubladas, Agua y El Junquito," Venezuela, December 29, 1936, at alt. of 1800 m.

Vernacular name: "*Canalete*" (Pittier).

*Z. australis* is noteworthy for its dark green thin leaves, large obovate strongly veined samaras 20 to 24 mm. long and 7.5 to 9.5 mm. wide, and cotyledons 2 to 2.1 mm. wide.

***Zinowiewia concinna*** sp. nov.—Arbor. Folia 4–8 mm. longe petiolata, subcoriacea, ovata, elliptico-oblonga vel lanceolata, 5.5–11 cm. longa, 2.5–4.5 cm. lata, apice abrupte acuminata, basi acuta. Cymae 1.3–2.5 cm. longae. Calyx profunde quinquefidus, lobis ca. 0.5 mm. longis, rotundatis. Petala 5, late ovata vel ovato-oblonga, 1.5–1.7 mm. longa, 1–1.2 mm. lata. Filamenta ca. 0.6 mm. longa. Antherae ca. 0.4 mm. longae. Ovarium in discum immersum. Fructus oblanceolati, 2–2.2 cm. longi, 6.5–7 mm. lati, acutiusculi, apiculati, venis debilibus. Semen 1; cotyledonibus lineari-lanceolatis, ca. 5.5 mm. longis, obtusis; radicula ca. 2.7 mm. longa.

A small tree (Pringle) or large tree (Hinton). Leaves subcoriaceous or subchartaceous. Petioles 4 to 8 mm. long, canaliculate. Leaf blades ovate, elliptic-oblong, or lanceolate, 5.5 to 11 cm. long, 2.5 to 4.5 cm. wide, apex acuminate, the acumen obtusish or acute, base acute, decurrent, costa nearly plane above or slightly impressed, prominent beneath, openly reticulate-veined, the main lateral veins 6 to 8 on each side. Cymes subsessile or short pedunculate, 1.3 to 2.8 cm. long, forked 4 to 6 times, the primary branches usually much shortened, crowded. Pedicels 2 to 3.5 mm. long, slender, jointed at or near the middle. Calyx 5-lobed, the lobes about 0.5 mm. long, the margins bearing slender red deciduous teeth. Petals 5, broadly ovate or ovate-oblong, 1.3 to 1.7 mm. long, 1 to 1.2 mm. wide, apex rounded. Filaments about 0.6 mm. long. Anthers about 0.4 mm. long. Disk pentagonal. Ovary submerged in disk; ovules small, about 0.25 mm. long. Fruits subfalcate, oblong-elliptic, 2 to 2.2 cm. long, 6.5 to 8 mm. wide, acutish or obtusish, apiculate, venation faint; seed linear-oblong, 8 to 10 mm. long; cotyledons linear-lanceolate, about 5.5 mm. long, obtuse; radicle about 2.7 mm. long, slender.

Type in the Herbarium of the University of Michigan, *C. G. Pringle* 8438, collected on Sierra de Tepoxtlán, near Cuernavaca, Morelos, Mexico, September 11, 1900, at alt. of 2450 m.

Additional specimens examined: MEXICO: Morelos, Sierra de Tepoxtlán, Feb. 8, 1899, *Pringle* 8024 (A, C, F, G, Mo, P, US-2); Sept. 11, 1900, *Pringle* 8438, type collection (A, C, F, G, Mo, NY, P, US-2); Nov. 20, 1902, *Pringle* 9706 (F, G, NY, Mo, US-2). Michoacan, Sta. Maria, Oct. 1909, *Arsene* (F). State of Mexico, District of Temascaltepec, Mina de Agua, alt. 1990 m., Oct. 31, 1932, *G. B. Hinton* 2332 (K, US); Feb. 4, 1933, *Hinton* 3253 (K).

Vernacular name: "*Gloria*" (Hinton).

Economic value: "Used in necessity for fodder" (Hinton).

The faintly-veined acutish wing of its oblong-elliptic samaras, the long pedicels, and the obtusish or acute acumen of the leaves distinguish *Z. concinna* from *Z. integerrima* (Turcz.) Turcz. to which it is very closely related. *Z. integerrima* has broadly oblanceolate or obovate rounded more strongly veined samaras, much larger cymes, shorter pedicels, and bluntly obtuse subacuminate leaves.

*Zinowiewia costaricensis* sp. nov.—Arbor. Folia 4–9 mm. longe petiolata, chartacea, parva, lanceolata, 3.5–8.5 cm. longa, 1.3–2.8 cm. lata, utrinque acuminata. Cymae ca. 1.5 cm. longae. Calyx profunde quinquefidus, lobis ca. 0.5 mm. longis, rotundatis. Petala 5, late ovata vel suborbicularia, 1.1–1.3 mm. longa, 1–1.1 mm. lata, apice rotundata, inconspicue erosa. Fructus oblanceolato-oblongi, 1.5–2.1 cm. longi, 5–6.5 mm. lati, apice emarginati. Semen 1 vel 2; cotyledonibus lineari-lanceolatis, 5.2 mm. longis, ca. 1.2 mm. latis, apice rotundatis; radícula 2.3 mm. longa.

A tree; branchlets slender. Leaves chartaceous, discolorous. Petioles slender, 4 to 9 mm. long, shallowly canaliculate. Leaf blades lanceolate, 3.5 to 8.5 cm. long, 1.3 to 2.8 cm. wide, apex and base acuminate, decurrent, much paler beneath, costa slightly raised above, prominent beneath, the main lateral veins 4 to 6 on each side. Cymes small, usually about 1.5 cm. long, forked 3 or 4 times. Calyx 5-lobed, the lobes rounded, about 0.5 mm. long. Petals 5, broadly ovate to suborbicular, 1.1 to 1.3 mm. long, 1 to 1.1 mm. wide, rounded at apex, inconspicuously erose. Margin of disk raised. Fruits oblanceolate, 1.5 to 2.1 cm. long, 5 to 6.5 mm. wide, subfalcate (1-seeded) or straight (2-seeded), venation of wing strongly ascending, faint, scarcely discernible near the margin, apex emarginate; 1-celled and 1-seeded, or 2-celled and 2-seeded, the seed erect, linear-oblong in outline, terete, 6 to 8 mm. long, apex rounded; cotyledons linear-lanceolate, rounded at apex, 5.2 mm. long, about 1.2 mm. wide; radicle 2.3 mm. long.

Type in the United States National Herbarium (No. 471,825), *Tonduz*

7861, collected on Cuesta de Terrazu, Costa Rica, at alt. of 1900 m. in April 1893.

Additional specimens examined: COSTA RICA, Cuesta de Terrazu, April 1893, *Tonduz 7861*, type collection (US-No. 577,182). Monte Candelaria, February 1847, *Oersted 116K* (F-fragment, US). PANAMA, vicinity of El Boquete, Chiriqui, alt. 1000 to 1300 m., March 2-8, 1911, *W. R. Maxon 5109* (F-2).

*Z. costaricensis* is noteworthy for having emarginate fruits 1- or 2-seeded, all the other species in the genus being strictly 1-seeded so far as known. The relatively small, discolorous, lanceolate leaves, acuminate at apex and base, distinguish the species further. The Oersted and Tonduz collections, excepting No. 577,182 (US), are homogeneous. In the Tonduz specimen, No. 577,182, apparently taken from a different tree than the type specimen, the fruits appear abnormal, being smaller than usual and obtusish. The leaves, however, are typical.

The Panama specimens, referred tentatively to *Z. costaricensis*, have leaves ovate or ovate-lanceolate, cymes as much as 3 cm. long, and petals slightly larger (about 0.2 mm. longer and proportionately wider). Young fruits are typically emarginate, but slightly broader; all of those available are 1-seeded.

***Zinowiewia Matudai* sp. nov.**—Arbor 7-9 m. alta, 15 cm. diam. Folia 7-11 mm. longe petiolata, chartacea vel subcoriacea, anguste oblonga, oblongo-elliptica, vel oblanceolata, 5-9 cm. longa, 2-3.5 cm. lata, apice acuminata, acumine obtusiusculo vel acuto, basi subacuminata. Cymae 1.4-2.4 cm. longae. Flores purpurei. Calyx profunde quinquefidus, lobis late ovatis, ca. 0.5 mm. longis, obtusiusculis vel rotundatis. Petala 5, ovata, 1.6-2 mm. longa, 1-1.2 mm. lata, obtusiuscula vel rotundata. Filamenta ca. 0.7 mm. longa. Antherae ca. 0.25 mm. longae. Ovarium in discum subimmersum. Fructus oblongi, 12-15 mm. longi, 4-5 mm. lati, apice obtusi, apiculati, venis debilibus. Semen 1, cotyledonibus lineari-lanceolatis, ca. 3 mm. longis, obtusis; radícula 1.2-1.4 mm. longa.

A tree 7 to 9 m. high, 15 cm. in diam.; branchlets slender, drying reddish-black, striate, slightly compressed at nodes. Leaves chartaceous at first, subcoriaceous with age, drying yellow-green, somewhat paler beneath. Petioles slender, 7 to 11 mm. long, canaliculate, reddish. Leaf blades narrowly oblong, oblong-elliptic, or oblanceolate, 5 to 9 cm. long, 2 to 3.5 cm. wide, apex acuminate, the acumen obtusish or acute, base subacuminate, distinctly callosed and revolute on each side, costa prominent beneath, slightly impressed above, openly reticulate-veined beneath, main lateral veins 6 to 8 on each side, prominulous beneath, inconspicuous above, arcuately ascending, anastomosing into a submarginal vein. Cymes 1.4 to 2.4 cm. long, pedunculate, forked 3 to 5 times, the branches short, crowding the flowers.

Flowers purplish (Matuda). Pedicels very short, usually less than 0.5 mm. long, jointed at or near the middle. Calyx 5-lobed, the lobes broadly ovate, about 0.5 mm. long, obtusish or rounded. Petals 5, ovate, 1.6 to 2 mm. long, 1 to 1.2 mm. wide, obtusish or rounded. Filaments subulate, about 0.7 mm. long. Anthers about 0.25 mm. long. Disk thick, pentagonal. Ovary almost entirely submerged in disk. Style slender, equaling filaments in length. Samaras oblong-elliptic, 12 to 15 mm. long, 4 to 5 mm. wide, subfalcate, the wing decurrent to base on side opposite seed, lateral veins above middle of wing nearly horizontal, faint, veinlets undeveloped from margins, apex obtuse or bluntly obtuse, apiculate; 1-celled, 1-seeded, the seed erect, lanceolate-oblong in outline, 4.5 to 5 mm. long, nearly terete, reddish; cotyledons linear-lanceolate, about 3 mm. long, obtuse; radicle 1.2 to 1.4 mm. long.

Type in the Herbarium of the University of Michigan, *Eizi Matuda* 1872, flowers and fruits, collected at Buena Vista, Escuintla, Chiapas, Mexico, January 1938.

Additional specimens examined: MEXICO: Chiapas, Mt. Ovando near Escuintla, Dec. 17, 1936, *Matuda* 424, flowers and fruits.

The callosed revolute base of the leaf blades, evident in the youngest unfolded leaves, is a peculiarity of this species. The yellow-green hue of the leaves, the purplish subsessile flowers, and the small fruits and seeds distinguish it further. Its closest relative is *Z. rubra* Lundell of Guatemala.

***Zinowiewia pallida*** sp. nov. (fig. 3).—Arbor glabra, 10 m. alta, 10 cm. diam. Folia 3–5 mm. longe petiolata, pallida, subcoriacea, oblanceolata, raro oblanceolato-elliptica, 4–9.5 cm. longa, 1.4–3.3 cm. lata, apice obtusa, raro rotundata, minute apiculata, basi acuminata. Flores parvi, pallide virides. Calyx profunde quinquefidus, lobis ca. 0.4 mm. longis, rotundatis. Petala 5, late ovata, 1.2–1.3 mm. longa, ca. 1 mm. lata. Stamina 5; filamentis ca. 0.5 mm. longis; antheris late cordatis, ca. 0.3 mm. longis. Ovarium in discum immersum. Fructus immaturus samaroideus.

A tree 10 m. high and 10 cm. in diameter, with short trunk; branchlets slender, red at first, whitened in age. Leaves pallid, subcoriaceous. Petioles reddish, 3 to 5 mm. long, slightly canaliculate. Leaf blades oblanceolate, rarely oblanceolate-elliptic, 4 to 9.5 cm. long, 1.4 to 3.3 cm. wide, apex obtuse or rarely rounded, minutely apiculate, base acuminate, slightly decurrent, discolorous, the young leaves whitish beneath, costa elevated above on lower half of blade, pinkish and very prominent beneath the entire length, main lateral veins 5 to 8 on each side, inconspicuous above, prominulous beneath, anastomosing near the margin. Cymes 2 to 2.8 cm. long, pedunculate, forked 4 or 5 times, open. Flowers small, pale green. Pedicel of terminal flower in cymules 1.2 mm. long, jointed at base; pedicels of lateral flowers in ultimate cymules about 2 mm. long, jointed at middle. Calyx 5-lobed, the lobes about 0.4 mm. long, rounded. Petals 5, broadly ovate, 1.2 to 1.3 mm. long, about 1



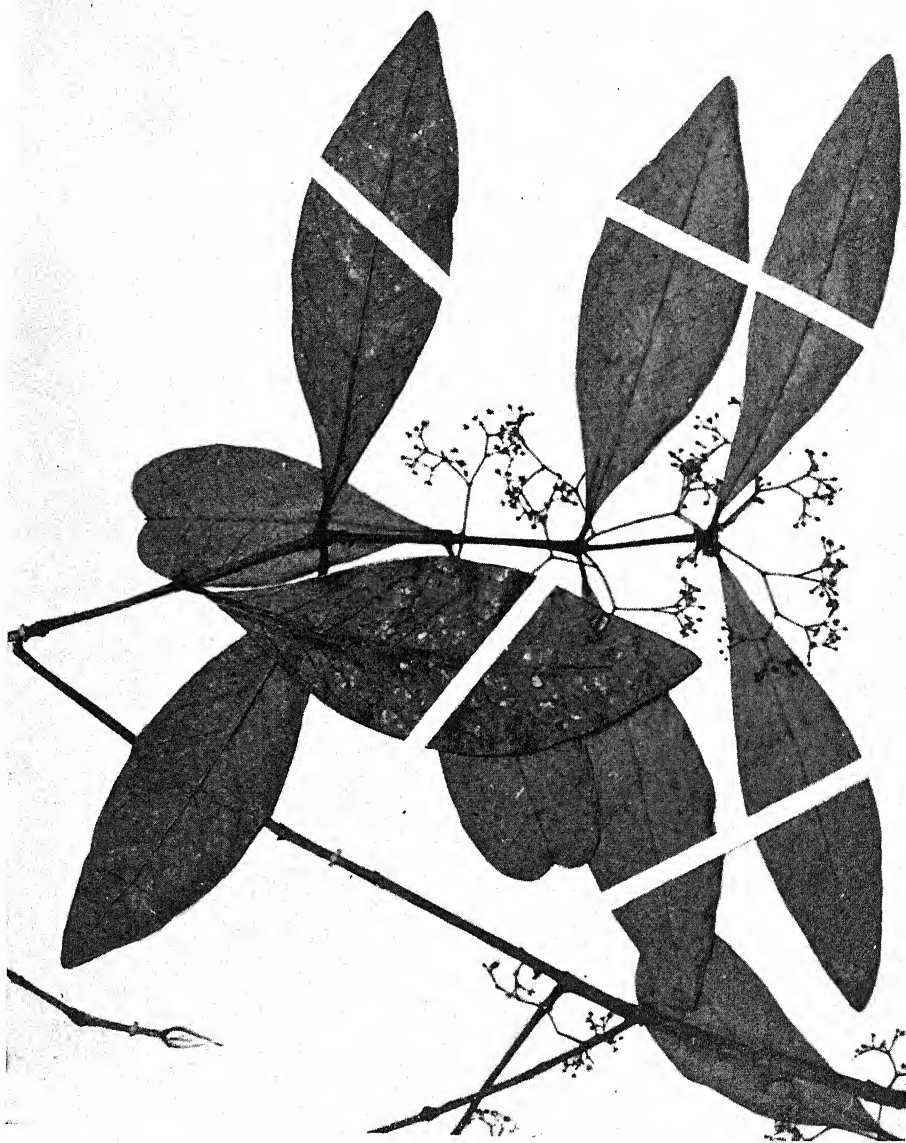


Fig. 3. *Zinowiewia pallida* Lundell. Type specimen (Lundell 6794), in Herbarium of the University of Michigan.  $\times \frac{3}{4}$ .

mm. wide. Filaments about 0.5 mm. long. Anthers about 0.3 mm. long. Disk thick, pentagonal, margin nearly plane. Ovary submerged in disk. Young immature fruits samaroid, typical of genus.

Type in the Herbarium of the University of Michigan, *C. L. Lundell 6794*, collected in open granite bed of Rio On, Mountain Pine Ridge, El Cayo District, British Honduras, Aug. 5, 1936.

In its obtuse rather than subacuminate or acuminate leaves, *Z. pallida* differs from all other species in the genus. It is evidently related to *Z. integerrima* (Turcz.) Turcz.

***Zinowiewia rubra*** sp. nov.—Arbor 30 m. alta, 75–90 cm. diam. Folia 3.5–11 mm. longe petiolata, subchartacea vel subcoriacea, lanceolata vel lanceolato-elliptica, 4–11 cm. longa, 1.5–3.5 cm. lata, acuminata vel subacuminata, acumine acuto vel obtusiusculo, basi acuminata vel acuta. Cymae 2 cm. longae vel breviores. Flores rubri. Calyx profunde quinquefidus, lobis late triangulari-ovatis, ca. 0.5 mm. longis, obtusis. Petala 5, ovata, 2–2.2 mm. longa, ca. 1.5 mm. lata, apice rotundata. Filamenta ca. 0.75 mm. longa. Antherae minutae, ca. 0.2 mm. longae. Ovarium in discum immersum. Semen 1.

A large tree; branchlets dark red, rather stout, internodes short or elongated. Leaves subchartaceous or subcoriaceous. Petioles 3.5 to 11 mm. long, reddish. Leaf blades lanceolate or lanceolate-elliptic, 4 to 11 cm. long, 1.5 to 3.5 cm. wide, apex usually acuminate, sometimes subacuminate, the acumen acute or obtusish, base acuminate or acute, decurrent, costa narrow above, pinkish and prominent beneath, openly reticulate-veined, the main lateral veins 5 to 8 on each side. Cymes 2 cm. long or less, short pedunculate or subsessile, the peduncles and branches stout, forked 2 to 4 times. Flowers crowded, maroon or tinged maroon. Pedicel of terminal flower in cymules about 1.2 mm. long, jointed at or above the middle; pedicels of all lateral flowers jointed above the middle. Calyx 5-lobed, the lobes broadly triangular-ovate, about 0.5 mm. long, obtuse. Petals 5, ovate, 2 to 2.2 mm. long, about 1.5 mm. wide, apex rounded. Filaments subulate, about 0.75 mm. long. Anthers minute, about 0.2 mm. long. Disk green, pentagonal. Ovary submerged in disk. Immature fruits oblong-elliptic, dull red (*Skutch 1680*), 1-seeded, obtusish.

Type in the Herbarium of the University of Michigan, *A. F. Skutch 639*, a tree 75 cm. in diam., flowers maroon with a green disk, in clearing above Tecpam, Department of Chimaltenango, Guatemala, alt. 2800 m., Oct. 14, 1933.

Additional specimens examined: GUATEMALA: Department of Chimaltenango, Tecpam, *Skutch 639*, type collection (D, NY, US). Department of Quiché, Nebaj, a tree to 30 m. high and 90 cm. in diam., flowers green tinged with maroon, fruits dull red, in remnant of cloud

forest, alt. 2550 m., Nov. 16, 1934, *Skutch 1680*, flowers and young fruits (F).

*Z. rubra*, the largest tree in the genus, may be easily recognized by its comparatively large maroon or maroon tinged petals as much as 2.2 mm. long and 1.5 mm. wide. It is closely related to *Z. Matudai*, but differs in its longer pedicels, larger flowers, green rather than yellow-green leaves, and the absence of the callosed revolute base of the leaf blades.

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## The emergence of smut-inoculated oat seedlings through sand and loam soil<sup>1</sup>

PAUL F. BRANDWEIN  
(WITH ONE FIGURE)

In experiments on the nature of smut infection in various oat varieties, the writer has observed the emergence through sand of seedlings inoculated with the loose smut, *Ustilago avenae* (Pers.) Jens., and the covered smut, *U. levis* (Kell. and Sw.) Magn. In experiments involving the use of approximately 10,000 seeds, half of which were uninoculated controls, there was 98.7 per cent emergence of plants from uninoculated seeds as compared with 97.2 per cent emergence of plants from seed inoculated with different races of smuts maintained at the Brooklyn Botanic Garden. However, Bayles and Coffman (1) have shown that dehulling reduced the emergence through soil of plants grown from uninoculated seed by 5.8 per cent and of inoculated seed by 10.6 per cent. Stevens (2) in field experiments reported that the smut-resistant Markton oat is injured by inoculation that results in the killing of many seeds and thus reduces the stand. After the seedlings emerge, however, there appeared to be no detrimental results. These observations pointed to the desirability of conducting experiments to discover some reason for these differences in emergence of seedlings through soil and sand.

The technique generally employed in this laboratory was used with the exception that seeds were planted in soil as well as in sand for purposes of comparison. The soil used was a good loam soil, screened through a 40 mesh sieve. The sand was similarly sieved through the same mesh.

In these experiments 110 cc. of soil or sand was placed in a waxed paper cup. The cup was then tapped several times on the table and ten seeds were placed at approximately equidistant points on this sand or soil base, and covered with an equivalent quantity.

Both sand and soil had a moisture content of 20 per cent of their water holding capacity and the cups were maintained at a constant temperature of 20°C. The ten seeds had been placed in coin envelopes and inoculated with about 10 milligrams of smut spores, the excess being spread as evenly as possible when planted. The dehulled seeds of the varieties Monarch and Markton were inoculated with the Missouri race of *Ustilago levis*, to which Monarch is very susceptible and to which Markton is highly resistant.

Four different plantings were made: soil only, sand only, soil base with sand cover and sand base with soil cover. All four sets were planted

<sup>1</sup> Brooklyn Botanic Garden Contribution No. 86.

simultaneously, 100 seeds being used in each set. The emergence of seedlings was recorded as follows:

	<i>Per cent emergence</i>	
	<i>Inoculated</i>	<i>Uninoculated</i>
Markton—Soil only	98	99
Sand only	100	100
Soil base, sand cover	99	98
Soil cover, sand base	100	100
Monarch—Soil only	98	98
Sand only	99	98
Soil base, sand cover	100	99
Soil cover, sand base	98	99

From the results, it seems clear that under these conditions, the emergence of the seedlings might be considered unaffected by soil, the slight difference in Markton being insignificant. However, these conditions do not simulate those present in the field. Plantings, therefore, were made in the field as described in a previous paper (3) with the exception that the seeds were immediately planted three inches beneath the surface of the soil. The rows of dehulled inoculated seed alternated with those which were inoculated. Two hundred seeds were used in each planting.

	<i>Per cent emergence</i>	
	<i>Inoculated</i>	<i>Uninoculated</i>
Markton—Plantings of April 10	90	96
Plantings of April 25	86	94
Plantings of May 22	88	94
Monarch—Plantings of April 10	80	88
Plantings of April 25	84	96
Plantings of May 22	80	92

From the field experiments there seems to be a definite reduction of the emergence through soil of plants from inoculated seed. The emergence of seedlings of Markton was reduced by 6.7 per cent and of Monarch by 10.7 per cent. This apparently confirmed the results of Bayles & Coffman (1) and of Stevens (2).

While no attempt had been made to tamp the soil other than to pat it firmly in place, careful examination showed that within a day or so, in the field, the soil had become packed to a varying extent in different portions of the experimental plot. This pointed to tamping as one of the factors which must be considered in evaluating the percentages of emergence of seedlings. Preliminary experiments were therefore begun with the added procedure that the soil or sand was tamped to simulate the observed condition of the soil in the field.

In sand, with light tamping (i.e., merely tapping the sand in place with



a wooden tamper) under the conditions of constant moisture and temperature previously described, there was 100 per cent emergence of Monarch and Markton seedlings from uninoculated seed as well as from seed inoculated with *U. levis*. Where a loam soil was allowed to settle on the seeds by tapping the waxed paper cups in which the germination was carried on, there was 98 per cent emergence of seedlings from inoculated seeds of Markton and 99 per cent emergence of the uninoculated controls. The

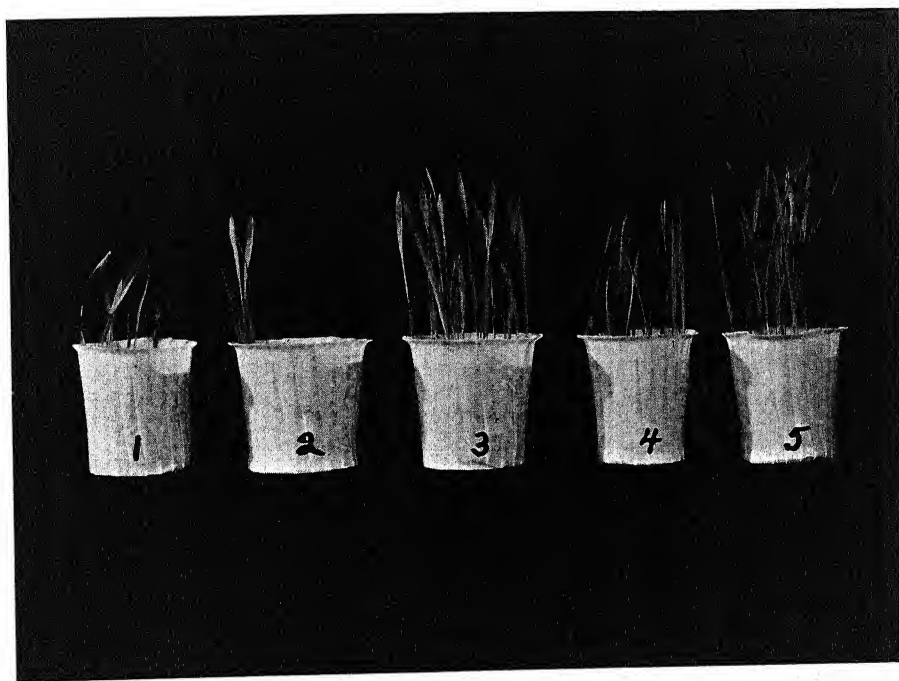


Fig. 1. Emergence of seedlings of Markton in heavily tamped soil and sand. (1, 2) inoculated with *Ustilago levis*, in heavily tamped loam soil; (3) the same, in heavily tamped sand; (4) uninoculated, in heavily tamped loam soil; (5) uninoculated, in heavily tamped sand.

Photograph taken 14 days after planting.

slightly lower emergence in soil as compared with sand may be accounted for by the various seedling-rot fungi which were present in the soil. However, when the loam soil was tamped as heavily as possible in the cups by pressing on the wooden tamper, so that the folds of the cup were slightly separated by the force used, there was a remarkable difference in the behavior of inoculated and uninoculated seeds. In such cases of heavy tamping, the emergence from inoculated seeds of the susceptible Monarch was reduced to an average of 55.5 per cent as compared with 82.5 per

cent emergence from the uninoculated controls. The emergence of plants of the resistant Markton variety was reduced to 75.3 per cent as compared with 90 per cent emergence from the uninoculated seed.

In sand, however, such heavy tamping had little effect in reducing emergence (fig. 1). In Markton, the emergence of inoculated seedlings through such heavily tamped sand (as described above for soil) was 98 per cent as compared with 98.5 per cent for the uninoculated. In Monarch, the emergence of the inoculated seedlings was 96 per cent as compared with 97 per cent for the uninoculated. In heavily tamped sand, the inoculated seedlings were in some cases slightly smaller on emergence as compared with the uninoculated; but after emergence grew to the same height as in the uninoculated (fig. 1). In soil, there was a marked difference in date of emergence; inoculated plants generally emerged one-half to a day later than the uninoculated controls.

In no case was the average emergence number of the inoculated seedlings higher than the uninoculated ones of any single cup in a given series of plantings. While this made these results significant, it was decided to attempt to control the tamping. Plantings were therefore made in vials 30 mm.  $\times$  100 mm. with one seed to the vial. All vials were carefully measured to insure equality of height, depth and width. Thirty grams of sand, previously prepared by screening through the 40 mesh sieve and by moistening to 20 per cent of the water holding capacity, was used as a base and an equivalent amount of sand used as a cover. Another vial which slid easily into the planting vial was weighted with enough mercury to make its total weight 300 gms. As soon as 30 grams of the moistened sand had been placed in the larger vial, the latter was gently tapped to permit the sand to settle. Then the weighted vial was dropped from a carefully measured height (within the larger vial) on the sand. This height was approximately 25 mm. from the top of the sand. Depending on the severity of the tamping desired, the vial could be dropped as many times as necessary. After the sand base was tamped, the inoculated seed was placed centrally and about 2 milligrams of smut spores were added in excess. At this time the 30 grams of sand was added as the cover. This was then tamped as before. The vials were stoppered with a plug of non-absorbent cotton which was placed as near to the surface of the sand as possible. All the vials were placed in an incubator at 20°, the air being maintained approximately at saturation from two containers of water.

Since previous experiments had shown that sand could not be tamped as tightly as soil, it was decided to use a very heavy tamping in order to obtain measurable results. After several trials, it was decided to drop the 300 gram vial 20 times and to permit the growth of seedlings for 10 days

in this tightly packed sand. They were then removed for measurement and subjected to various other examinations dealing with the extent of smut infection. A control consisted in tamping the sand twice with the mercury weighted vial. The control seedlings were measured after three days, just before emergence.

The results obtained are summarized in table 1. It seems clear that there is a difference between the inoculated and non-inoculated plants under heavy tamping. Under light tamping in sand there is no difference

TABLE 1

*Influence of tamping on the emergence of seedlings of Monarch and Markton oats inoculated with Ustilago levis, and non-inoculated controls.*

VARIETY	PER CENT GERMINATION	AVERAGE HEIGHT IN MM.
<i>Series A—tamped 20 times</i>		
MONARCH		
Inoculated	75	16.3
Non-inoculated	95	25.0
MARKTON		
Inoculated	85	20.1
Non-inoculated	100	25.3
<i>Series B—tamped twice</i>		
MONARCH		
Inoculated	100	10.3
Non-inoculated	100	9.6
MARKTON		
Inoculated	100	11.8
Non-inoculated	100	12.8

In each experiment 40 seeds were planted.

The seedlings in Series A were measured when 10 days old, and those in Series B when 3 days old, in both series before emergence.

between the two. The latter fact bears out countless observations carried out in the Laboratory of Plant Pathology of the Brooklyn Botanic Garden.

It is suggested that the marked smaller size of the inoculated seedlings of both the susceptible variety Monarch and the resistant variety Markton is in some measure due to the coleoptile invasion which has been found (3, 4, 5) to be present in resistant as well as susceptible varieties. Undoubtedly, in Monarch, and in Markton to a much lesser extent, the further mycelial penetration of other plant tissues plays some part in retarding the emergence of the plant under pressure. In Monarch, the mycelial invasion of the other plant tissues by *U. levis* is rapid. In Markton, too, Smith and Bressman (6) have reported several cases of smut sporulation when that variety was inoculated with various races of the covered

smut. In addition, Western (5) has shown some infection of the coleoptile and mesocotyl of Markton when inoculated with the covered smut; he did not note any infection of the growing point. The present writer (3) has noted at least one infection of the growing point of Markton by *U. levis*, and since then has had occasion to note two other cases of infection as evidenced by the sporulation of the smut. However, it appears (3, 4, 5) that for the great majority of resistant plants, the mycelium does not go further than the coleoptile. From observations made by Western and by the writer, it seems further evident that the extent of infection of the coleoptile of susceptible plants is much greater than that of resistant plants. Indeed, in the latter the infection sometimes is found to consist of a few attenuated and disorganized hyphae. It seems clear, however, that in resistant plants, the extent of the invasion by the mycelium may vary considerably.

In emergence, it appears to be the coleoptile which shields the tissues as the plant pushes through the soil or sand. It may be that the coleoptile is weakened by the mycelial invasion so that it cannot penetrate as effectively as does the uninoculated plant through tamped loam soil which furnishes the resistance that loosely tamped or loosely adhering particles of soil or sand do not present. This tamping effect may help to furnish a partial explanation of the results of Bayles & Coffman (1) and Stevens (2). In any case, my results point to the advisability of taking this tamping effect into consideration where experiments designed to test the susceptibility or resistance of an oat variety are conducted. In this Laboratory, preliminary plantings are made in loosely tamped sand in paraffin cups under constant moisture and temperature. After emergence the seedlings are transplanted to the field. In this manner, any adverse effects of tamping, damping-off fungi, shifting temperature, undependable conditions of moisture, are obviated. Furthermore, maximum infections are obtainable when this technique is used.

Many thanks are due to Dr. G. M. Reed for the material and the advice he has so unfailingly and generously given.

#### SUMMARY

Under severe tamping, the emergence of smut-inoculated seedlings of both susceptible and resistant oat varieties is reduced as compared with their uninoculated controls.

It is suggested that the coleoptile infection found by Kolk, Western and the present writer, to be present in inoculated resistant and susceptible oat varieties may be responsible for the failure of these plants to penetrate such tightly packed soil.

Examination of seedlings under heavy pressure shows a smaller size and lower germination of the inoculated plants as compared with their non-inoculated controls. Both Monarch, a susceptible variety, and Markton, a resistant form, showed similar reactions.

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BROOKLYN BOTANIC GARDEN

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## Salt spray: An important factor in coastal ecology\*

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(WITH THREE FIGURES)

### INTRODUCTION

Everyone who has visited sea coasts has noted the marked modification of form of woody plants close to the ocean; these are greatly repressed on the seaward side having a characteristic sloping form which has been universally called "wind form." The axes of the repressed shrub masses and of the one-sided trees are always in the direction of the strongest winds from the sea, which along most of the eastern U. S. coast are northeast (figs. 1 and 2).

The term "wind form" has not only had the descriptive connotation but the causal one as well. In *Plant Sociology* of Braun-Blanquet and Fuller (1932) is a statement and an illustration pointing to coastal winds as the cause of "wind form." Weaver and Clements in their *Plant Ecology* (1938) state, "On wind swept coasts and on high mountains excessive water loss results in a stunted and gnarled growth. This is, however, partly due to the mechanical effect of the wind." These books reflect the apparently obvious conception held by all observers to date, that wind is the factor involved.

The only report we have been able to find indicating injury by salt spray is that of Boodle,<sup>1</sup> who reaches the conclusion, "that the scorching of foliage by sea winds is chiefly due to the drying action of the wind but the salt may perhaps occasionally contribute toward the production of an injurious effect."

It is the purpose of this paper on the basis of observations made during the spring of 1937, to show that the "wind form" is not due to wind *per se* but to the salt spray carried by the wind, killing the growing shoots. This study brings to the front a factor almost unrecognized, yet of the greatest importance in coastal plant ecology.

### THE EVIDENCE

On the North Carolina coast, with the exception of the low sea-elder shrub (*Iva imbricata*), no woody plants occur on the dunes next to the strand. Here the sea oats (*Uniola paniculata*) is strongly dominant accom-

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<sup>1</sup> Boodle, L. A. The scorching of foliage by sea winds. *Jour. Ministry Agri. Great Britain* 27: 479-486. 1920.

panied by a few other herbs highly distinctive of this most exposed sea front zone. The woody plants occur on flats or low sandhills behind the sea front dunes.

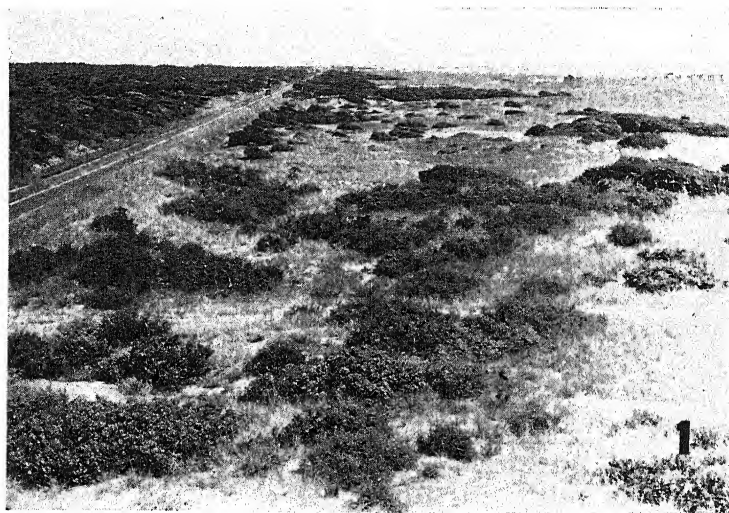


Fig. 1. Spray forms (formerly called "wind forms") *Myrica cerifera* and *Ilex vomitoria* near Fort Fisher, 20 miles south of Wilmington, N. C. Spray repressed *Pinus Taeda* on left of road.

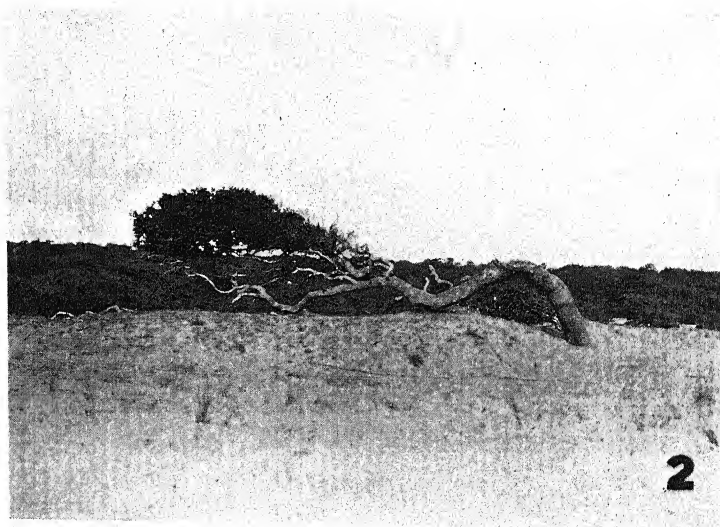


Fig. 2. Extreme spray form of *Quercus virginiana* near Nags Head, N. C., 55 miles north of Cape Hatteras.

Working on the seaward side of the Cape Fear peninsula below Wilmington, North Carolina, on April 16 we tagged a number of the new shoots of various "wind form" shrubs and trees found in this arboreal zone (fig. 1).

On April 30 we were surprised to find severe injury to the new shoots which occurred uniformly on the southeastern sides of the shrub masses. This definitely indicated some cause associated with a high southeast wind. The injury consisted of the killing of the upper younger tissues of the stems, the small immature leaves and the margins of the half developed leaves lower down, the necrotic areas of the latter appearing in a definite marginal pattern, extending proximally from the tip. It was noted that the most injured shoots were those most exposed. Those which were even slightly protected in shallow depressions in the compact shrub face, showed little or no injury. Upon checking the wind records at the Wilmington Weather Bureau Office (18 miles distant) we found a southeast wind of a relatively high intensity recorded for a period of 19 hours extending from the evening of April 24th to the afternoon of the 25th. This wind at the city station, 12 miles from the ocean, reached a maximum velocity of 28 miles per hour, the average, however, being 15.4 miles per hour. The seaside intensities would probably be much higher than these. No other wind approaching this one in duration or intensity occurred during the two-week interval. The sky during the high wind period was cloudy, and the soil water had been high in consequence of the frequent rains of the spring season. These two conditions eliminated the drying effect of the wind as a killing agent, forcing the conclusion that the injury must be ascribed to the salt spray carried in the wind.

Fortunately near the site of our original observations, nature arranged a perfect demonstration of this salt spray effect. Just south of the old Fort Fisher, relic of Civil War days, the peninsula suddenly narrows to little more than the width of the ocean strand and dune, due to the presence there of an estuary of the Cape Fear River. Stretched across the peninsula in front of this bay and facing directly to the southeast was a zone of the familiar coast shrubs dominated by the wax myrtle (*Myrica cerifera*) (fig. 3). A close examination of this shrub zone gave perfect confirmatory evidence that the further away from the sea a plant was located, the less noticeable was the injury. The first shrubs on which no injury was detectable were 280 yards (.16 miles) from the sea, as measured on a direct line east from the ocean, and about  $\frac{1}{2}$  mile from a point where a southeast wind could pick up the spray from the surf. Many of these uninjured shrubs were well isolated on the salt meadow fully exposed to east and southeast winds yet they showed not the slightest tendency to

a slope form in relation to the sea winds. Thus the southeast-facing shrub zone gave conclusive evidence of the role of the spray factor.

One observation still puzzled us. It was repeatedly noted on the repressed sea-front shrubs that, where the young and tender shoots were slightly depressed in the compact surface of the fastigate twig mass, little or no injury occurred. So shoots of approximately equal surface area were taken from exposed and slightly depressed positions and carefully washed with equal amounts of distilled water. A few drops of silver nitrate solution were added to each of the washings. That from the exposed shoot gave a strong chloride precipitate, while that from the depressed shoot gave barely a trace. Why shoots so slightly depressed should escape from the spray, was puzzling until it was realized that a strong wind playing over a porous surface would set up a suction effect comparable to that familiar in atomizers, an effect which would result in a slight elevation of the spray-laden wind above the short spring growth slightly depressed in the shrub mass. A similar effect would keep the spray from falling behind the shrub mass, permitting the leeward lateral shoots to grow unimpeded. This phenomenon means that during the period of strong winds from the sea, there is set up a ground air current toward the sea. This air moves up through the interlacing branches and not only keeps the spray from settling into the shrubs but actually elevates the spray-laden wind slightly above their sloping surfaces. This effect is naturally most pronounced nearest the sea where the wind velocity is the highest, and where the spray is most concentrated.

At the same period in which all of the foregoing observations were made, we were able to produce exactly the same type of injury by spraying healthy juvenile shoots of wax myrtle, yaupon and live oak once or twice with sea water, and with distilled water containing a 3 per cent concentration of sodium chloride. The injury patterns resulting in both cases were identical with that from sea spray.

In contrast to these observations attention should be called to the fact that, where the wind sweeps across the sound estuaries of fresh water with little less velocity than it does over the ocean, no noticeable modification of the shore woody plants is discernible. Careful examination of those on the west shore of the Chowan River, 2 miles in width, showed not the slightest deviation from a uniformly symmetrical form among all the woody plants.

From the foregoing evidence, it is clear that a complete revaluation of the wind factor in coastal plant ecology must be made. Certainly on the coast of the Cape Fear peninsula, we can state categorically that the so-called "wind formed" shrubs are not wind formed at all but owe their

marked modification wholly to the killing action of the salt on the tender shoots during their growing period. These coastal malformed shrubs should therefore be called "spray forms."

#### NATURE OF THE INJURY

It may be assumed that, during the day-time exposure to spray, the concentration of the chlorides deposited on the plants is always higher than that of the sea water, owing to the rapid evaporation of the water by the high wind occurring at that time.

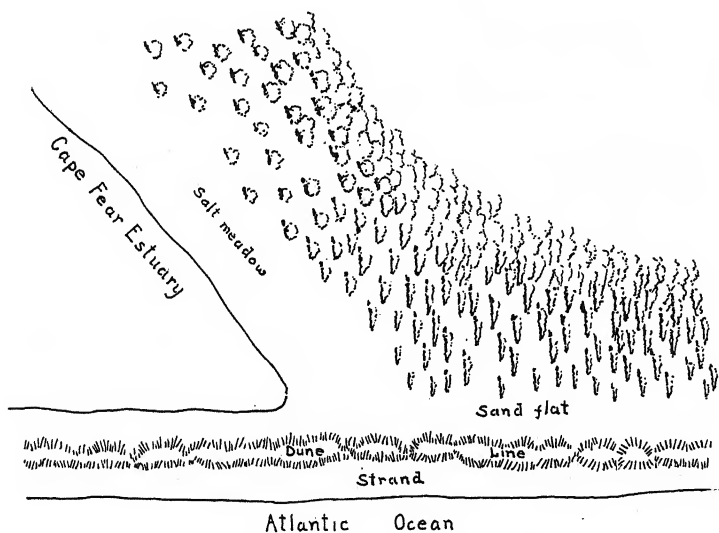


Fig. 3. Section of coast south of Fort Fisher, N. C. Slope form shrubs only in spray zone. Those exposed to wind across estuary but beyond spray zone are of normal form.

Since killing of very young tissues of the new shoots could readily be induced by one or two applications of sea water in the day period it is clear that the longer spray exposure would result in severe injury to the immature tissues. Only the adult stems and leaves escape in the case of the plants found in the stronger spray zones.

The injury may thus be interpreted as necrosis due to excessive water loss from the young tissues resulting from the osmotic action of high salt concentrations on the unprotected surfaces.

#### DIFFERENTIAL RESISTANCE OF COASTAL PLANTS

The most resistant woody plant is the water bush (*Baccharis halimifolia*). This fact, however, does not necessarily mean that this shrub will



be found nearest to the sea, because its distribution is also partly controlled by the depth of the water table. It is never seen growing on the dry sides of dunes or even slightly elevated areas. Next in order of resistance are the yaupon (*Ilex vomitoria*) and the wax myrtle (*Myrica cerifera*) which are equally tolerant of salt spray; they are frequently seen merged in common shrub masses.

The only tree on the sea front associated with the shrubs mentioned is the live oak (*Quercus virginiana*) which, assuming a compact shrub-form, is sparingly scattered in the fully exposed zone, but occurs for the most part protected by one or more of the preceding shrubs. On the coast facing northeast, in the vicinity of Kitty Hawk, a shift in the dunes occasionally leaves a live oak exposed to the full force of the ocean wind with its high content of salt spray. This results in a completely one-sided development (fig. 2); new growth being impossible on the spray exposed side, the tender shoots survive only on the protected side of the tree. Such trees show the maximum attainment of the spray form.

Most sensitive of all the arborescent species surviving in the spray zone is the loblolly pine (*Pinus Taeda*). An occasional low specimen was noted in the front zone, but it was always behind a protecting shrub mass.

Through field observations and many tests we found that the young growth of loblolly pine was readily killed under weak spray intensity, but the mature leaves either of the current season or a year old were somewhat resistant. There is a lag in the appearance of the characteristic light sienna color of the necrotic leaves following the application of the salt water. Their tips first show the injury, the necrosis rapidly progressing stemward until the leaves are completely killed. This is then followed by dehiscence of the branch. The observed behavior of the leaves artificially sprayed and dipped in sea water checked with conditions found in the field. In the Fort Fisher area, *Pinus Taeda*, characterized by a slight resistance to the salt, dominated the inner and weaker spray zone.

The only five woody plants occurring and persisting in the spray zone listed in the order of their resistance are water bush, yaupon and myrtle, live oak, and loblolly pine.

Observations on a few representatives of more inland woody plants (persimmon, turkey oak, grape) which by chance were close enough to the sea to be injured showed such a severity of injury to the practically mature leaves that the explanation of their almost complete absence from the spray zones was apparent.

Extensive areas of the turkey oak (*Quercus Catesbaei*) occur along the coast near the sea. Why these trees, so perfectly adapted to the sand soil

habitat, never were found competing with the woody plants of the seaside, had been puzzling to ecologists. Our observations solve this problem. The leaves of this tree cannot even tolerate the weak spray of the inner zone, which is withstood by the pine.

In all of the woody plants except the pines, branch regeneration from lateral buds occurred throughout the growing season. The new growth was not confined to the spring period. Thus the degree of fastigation in any particular zone is related to the frequency of high winds with their high spray content.

#### SPRAY ZONE WIDTH

Having learned that the loblolly pine along the coast was the most sensitive of the woody plants able to survive in the weak or landward side of the spray zone, we were able to use this tree as an index in measuring the width of the spray zone at various points along the coast. Myrtle Beach, South Carolina, showed the narrowest width (lowest winds) with a measurement of .1 mile. The Orrell line road transect near Fort Fisher gave .3 mile. The widest spray zone perhaps on the entire coast was that noted at Kitty Hawk on the northeast-facing coast below Norfolk where injury was apparent 1.25 miles inland.

#### SALT SPRAY AND THE DUNE COMMUNITY

From the observations presented on the restricted number of woody plants able to survive in the salt spray zone compared to the number of woody plants which cannot exist in this zone, it would seem to follow that the same contrast must obtain in relation to the dominantly herbaceous dune community. And this would be especially true since this community occupies the heaviest spray zone of all, that next the strand. To test this matter we transplanted a clump of wire grass (*Aristida stricta*) from an inland sandhill community dominated by long leaf pine and turkey oak to a dune top on April 3. On April 9 almost all the leaves had been killed nearly to the base, and on April 30 the plant gave evidence of being completely dead. Another clump placed 30 yards inland from the strand showed little injury during the month's exposure.

It seems probable that the distinctive composition of the dune community is based primarily upon the species adaptations to the spray factor. However, much more work must be done on this phase of the problem before a completely satisfactory evaluation of the front dune factor complex may be reached.

#### SUMMARY

Observations made during the spring of 1937 prove that the repressed

sloping forms of the seaside shrubs ("wind forms" of the literature) are not due to wind but to the killing action of salt spray on the young growing shoots. Such form modifications should therefore be called "spray forms."

Based upon the death within a month's period of *Aristida stricta* transplanted from an inland habitat to the front dunes, it is suggested that the dominants of the ocean dune community are dominant because of their resistance to salt spray.

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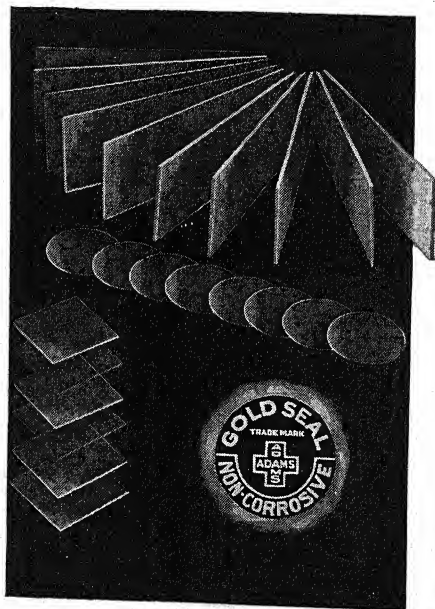
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## Spiral Systems in the Vascular Plants<sup>1</sup>

JOHN H. SCHAFFNER  
(WITH PLATES 22 TO 24)

The sporophytes of vascular plants usually develop a radially symmetrical stem or axis from a meristematic mass of dividing cells. This radial symmetry depends on a fundamental potentiality possessed by the interacting cell group. The bud, with or without an apical cell, not only develops the stem cylinder but in practically all living species also produces lateral appendages, or leaves, in the axils of which axillary buds may or may not be present. The fundamental, radially symmetrical system is also present in the sporophytes of all Bryophyta, altho they do not develop lateral appendages, except the expanded hypophyses of some mosses which may be regarded as continuous lateral appendages whose growth is also controlled by the inherent radial potentiality of the developing system. In the majority of Bryophyta the gametophyte has also evolved the radial potentiality and its superficial lateral appendages, or scales, are also developed in radially symmetrical spiral systems. The fundamental radial symmetry of the sporophyte may be modified so that the stem develops as an oval, quadrangular, triangular, or even decidedly flattened system, but such forms are secondary developments and the plant still shows the primary cylinder at various stages of its growth. When the sporophyte stem develops leaves they are so determined in their positions that after growth is completed, they form a spiral system of greater or less complexity and of greater or less mathematical regularity.

The spiral system is not only a characteristic of the leaf arrangement, or phyllotaxy, but involves also the structure of the vascular system and other tissues in the stem. The spiral structure is prominently in evidence in the skeletons of old stems of the tree prickly-pear, *Opuntia imbricata* (Haw.) Engelm., in which the specific spiral system can be determined as readily from the large gaps in the vascular cylinder as from the external leaf positions. The branches of *Cercis* and *Pedilanthus* and of many other plants show a zig-zag character in harmony with their alternate two-ranked leaf arrangement. The correspondence between the structural organization of the twig and leaf arrangement is clearly indicated by the five-angled pith and the five ridges on the bark of cottonwood twigs, *Populus balsamifera* L. The same relation is also prominently shown in young shoots of various species of blackberries, as in *Rubus frondosus* Bigel., by the five-angled pith and the five very prominent ridges on the

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stem. Thus, it is evident that the leaf positions and the structural relations of the stem are primarily determined by the same fundamental potentiality. There is a fundamental potentiality of spiralization which determines the relative positions of the leaf incepts and the correlative interactions of these centers of growth activity in relation to each other and also determines the general arrangement of the tissue systems throughout the total mass of cells of the growing bud. The addition of a further potentiality to the hereditary complex which causes the production of internodes does not change the general spiral system but is to be regarded as only a third advance in the progressive complexity of the sporophyte stem along with the fundamental radial symmetry and potentiality for spiralization.

What the ultimate nature of this potentiality of spiralization may be cannot be surmised at present, but it is, nevertheless, something quite as definite as the force of crystallization in the various chemical substances. It is some internal correlative or coordinating interaction force or potentiality which determines the physiological gradients of the bud and the structural positions of the new incepts for leaves or other lateral organs as the growth of the bud proceeds. One thing is certain; the positions in the spiral systems are not primarily dependent on any predetermination of the structural elements of the stem already laid down, since the system may change in any given bud from one type to another. The differentiation of the structural elements is determined by physiological or physico-chemical forces in action at the time of growth. Thus, very profound reaction changes are especially in evidence when a bud changes from an alternate, two-ranked, vegetative system to a reproductive, trimerous or pentamerous system in the flower. Whatever the factors involved may be, the final result is produced by a combination of all the growth forces and growth processes active in the given system.

By controlling the ecological-physiological conditions, the writer was able in the hemp plant, *Cannabis sativa* L., to cause a change from opposite to alternate leaf arrangement at any level of stem development beyond the few opposite nodes which had already been determined in the plumule of the embryo. After rejuvenation of old plants the alternate leaf arrangement also frequently changes back again to the opposite condition (Schaffner, 1926). The change from one vegetative spiral system to a succession of others during the ontogenetic growth gradient is easily seen in many common plants.

Recently it has become the vogue to attempt to explain all growth reactions on the basis of hormones and growth-promoting substances, but such agents can only be secondary in the determination of spiral systems. The accumulation of hormones may stimulate cell division at certain

points but the real problem is to discover the mechanism which determines the mathematical positions where the substances accumulate, if there is such a relation between growth and the supposed stimulating substance.

There is at present much superficial reasoning about the influence of cosmic rays, violet rays, temperature, etc. as primary causal agents of evolution, but a study of the spiral systems as well as of numerous other biological systems in relation to the general taxonomic system shows that all such reasoning is beside the mark. There is no evident correspondence between the presence of the supposed causal agents and the systems themselves. For example, the grasses, numbering over 4,000 species, with numerous tribes, subtribes, and genera, have been on the earth for an enormous period of geological time and at present extend from the Equator to the Arctic regions, from the water to the desert, from sea level to the vegetation limit of high mountains, yet they all have the alternate, two-ranked spiral system in their vegetative shoots. The sedges are close lower relatives of the grasses and are nearly as widely distributed over the earth, often growing in the same habitats and thus subjected for ages to the same physical agents—heat and cold, violet rays, cosmic rays, etc.—as the grasses, but this has not given them the same spiral system. The vast majority of them have the spiral three-ranked leaf arrangement, frequently with three-angled stems. A few species have their leaves arranged in complex multispirals.

By various authors, as in Schwendener's mechanical hypothesis, the stimulus determining the positions of the incipient leaf members was assumed to be the pressure exerted by the developing leaves covering the growing bud. But such an explanation represents a purely superficial view, since many stems with only minute, vestigial leaves have very definite spiral systems, as in many cacti and spurge.

When one studies various phylogenetic series, it soon becomes evident that in the lower levels of the series there is frequently much variation in the number of spirals produced even on the same stem and between branches of the same plant, and that the control of the spiral development goes thru certain evolutionary sequences, which at the higher levels commonly end in one of a few determinate, stable systems, unless some unusual hereditary factor is introduced, such as a special expansion potentiality active either in the vegetative or reproductive phase or in both. These culminating systems become practically fixed and unchangeable in entire families or even larger groups and are of great importance in determining taxonomic relationships.

Apparently the lower vascular plants had comparatively simple spiral systems, as is the case in the living species, and these became more com-

plex in various lines thru the progressive evolution of larger buds with no corresponding increase in the efficiency of the internal correlative control or coordinating interactions from the centers of activity to the surrounding cells. Thus, the larger the bud the greater the number of spirals produced at any given level, and thus sometimes an enormous difference on stems, branches, or flowers of different sizes, as is prominently shown in nearly all species of *Equisetum*. With the evolutionary advancement in the efficiency of the correlative control from the determined centers, the vegetative spiral system will be simplified again on the higher evolutionary levels even tho there be a decided increase in the size of the growing bud. Two prominent culmination types become established in many phyletic lines of Pteridophyta, Gymnospermae, Monocotylae, and Dicotylae. The two normal culminations or determinate types are (1), the alternate, two-ranked arrangement, in which the center of activity has the largest controlling influence possible in a radially symmetrical system, taking in the entire cross-section at the given growth level; and (2), the opposite, four-ranked system which becomes the normal, determinate limit when the pitch of the clockwise and counter-clockwise primary spirals becomes the same, with the centers of activity at each node reduced to the smallest symmetrical number, namely two. Unusual or abnormal, extreme systems are the opposite two-ranked arrangement and the unispiral system. Both of these are very rare. An advanced system may be evolved in the plant which may be expressed only at a certain stage of the ontogeny. Thus, in *Cyperus* the extreme, two-ranked condition appears only in the branches of the inflorescence. In some species of *Helianthus* the opposite, four-ranked system is developed in the juvenile stage while in the later periods of growth the five-ranked arrangement is expressed. The same is true for the hemp, *Cannabis sativa* L. Thus it must be recognized that a more recently acquired spiral reaction system may come to expression either in the early juvenile stage or in the later growth stages of the ontogeny.

It is an interesting fact that the growth of true roots rarely if ever shows an indication of a definite spiral control. The root branches seem to develop in a rather haphazard fashion. The potentiality for spiralization seems to be completely latent, altho as soon as a stem bud develops on a root it immediately begins a spiral activity, shown by the spiral arrangement of its lateral organs. In *Stigmaria* fossils, which represent branched stems penetrating the ground like root systems from the base of the tree trunk, the root-like structures have the positions of leaves in spirals and probably have some relation to leaf structures.

Elaborate systems of phyllotaxy have been developed, but these have dealt especially with abstract mathematical and philosophical theories on

the one hand or on the other with fantastic teleological speculations as to the causal relations of the different spiral systems to their environments or to supposed special advantages of one type or another of leaf arrangement to the individual. There was little of practical value in these speculations, and Sachs was inclined to dismiss the subject from serious consideration as "playing with figures." But these rhythmical processes of growth are a very prominent part of the phenomena of life and as such demand study from various points of view. The abstruse and complicated mathematical treatments and speculations could not arouse very much enthusiasm in the non-mathematical botanists, who both in the past and at present constitute nearly the entire taxonomic clan.

The general system of phyllotaxy still in vogue lays especial stress on the angle of divergence, or the proportion of the distance around the stem that one leaf is removed from the one next in age, as in the Fabonacci series but the sequence of the order of appearance may be considerably changed thru various causes and thus cannot be used, except in the simplest systems, as a basis for fundamental mathematical speculations. The ontogenetic gradients may be modified by determinate factors, by zygomorphic or inequilateral factors or by expansion factors at various points of development. In the more primitive type of typical flowers, as in *Lilium* for example, the members appear in acropetal succession. In advanced types the cycles are often practically synchronous in origin. In some, the incepts of the carpels may appear before those of the stamens, or the incepts of the sepals may develop after those of the stamens. In *Capsella* the petals are the last to appear. In zygomorphic flowers there is often a decided difference in the appearance of the incepts of the members of a single cycle. But these changes in sequence of the ontogenetic development do not change the fundamental nature of the spiral systems involved, and one cannot tell from the matured structures in what sequence the different members originated. From a practical point of view, we are more especially interested in the character of the completed systems and should deal with them as such. Nor are we concerned whether the systems are mathematically exact. They can at best be only approximate. The exact mathematics of any material system is only in the mind of the mathematician. Flattened stems, as in some species of *Opuntia*, may still show an evident spiral system. Dorsiventral shoots are due to secondary potentialities which are imposed on the more primitive radial systems and the typical cylindrical spirals are thus modified, but such cases do not at all invalidate the spiralization as a fundamental system.

The subject of phyllotaxy also developed a difficult terminology with such terms as divergence angle, orthostiches, parastiches, decussate, genet-

ic spiral, genetic cycle and Fabonacci ratios. The "cycle" is defined as the portion of the genetic spiral between any two leaves directly above one another, a meaning quite different from that in general use when a flower is said to be cyclic, tricyclic, pentacyclic, etc.

The so-called Fabonacci series of fractions, named from its discoverer, is as follows:  $1/2$ ,  $1/3$ ,  $2/5$ ,  $3/8$ ,  $5/13$ ,  $8/21$ ,  $13/34$ ,  $21/55$ , etc. It corresponds to a selected list of ratios that can be found in the spiral systems of plants, but, as will appear below, the system as a whole is very much more complex. This Fabonacci series of fractions was in the past even compared with a somewhat similar series of approximate numbers representing the relative distances of the planets from the sun, usually known as "Bode's law."

The teleological explanations given in the past for the various systems of phyllotaxy are, as would be expected, commonly extremely absurd and inconsistent. The Fabonacci relation being the commonest, it was assumed to be possibly the most primitive type. Another especially fantastic notion has been held that the present spiral systems of the vascular plants are the outcome of a long series of progressive adaptations. Bonnet assumed that the spiral arrangements gave the optimum advantage for transpiration, while Wiesner gave an equally fantastic teleological explanation, that the Fabonacci relation gives the optimum angle for maximum exposure to light in photosynthesis. Such teleological explanations are easily laid to rest when one has advanced far enough in taxonomic studies to learn that similar spiral systems are present where the leaves are vestigial or are reduced to minute scales, as in many cacti, milkweeds, spurges, etc., and as in the scale leaves on the ordinary branches of *Pinus*, the bracts on the cup of the fruit in *Quercus*, and the scales on the surface of the pericarp of the fruit of some palms as in *Raphia* and *Calamus*. As well might one seek to find a teleological explanation for the angles of the various species of crystals of chemical compounds.

#### A SIMPLE METHOD FOR REPRESENTING SPIRAL SYSTEMS

After many years of taxonomic study and teaching of advanced students, the writer has attempted to develop a simple, definite, and practical method for constructing projection diagrams of all types of spiral systems, whether simple or complex, and also to devise a system of numerical formulae that would indicate the complete and exact nature of the various types and their ordinary modifications. The aim was especially to develop a system that could be used conveniently for both vegetative shoots and flowers. In the present paper the intention is to present the simple facts of the spiral systems so that the more important patterns can be used con-



veniently in systematics and in the discovery of evolutionary trends, sequences, and limits in the various phyletic lines.

All normal types of mature spiral systems, developed on a cylinder, contain four main morphological characteristics: (1) one or more clockwise primary spirals, (2) one or more counter-clockwise primary spirals, (3) two or more ranks, or radii, either straight or spiral, and (4) one or more secondary spirals whenever the clockwise and counter-clockwise primary spirals are unequal in number; or if the primary clockwise and counter-clockwise spirals are equal in number there are no secondary spirals but the leaves or other members are in cycles. Explanations of these terms are given below. Since the various spiral systems all have these four characteristics, they can all be represented by a formula of four numbers with dashes between them. The clockwise primary spirals are always written first; the second number represents the counter-clockwise primary spirals; the third number represents the ranks or radii; and the fourth number represents the secondary spirals or indicates that the system is cyclic. The direction of the spirals is always to be determined in the direction of growth, namely from the bottom of the shoot to the top.

#### METHOD FOR CONSTRUCTING PROJECTION SPIRAL DIAGRAMS

The procedure for making a projection diagram of a spiral system is as follows: Take, for example, a comparatively simple spiral system as represented in a twig of *Populus balsamifera* L. (Cottonwood), a young shoot of *Rubus frondosus* Bigel., a long potato tuber of the "Idaho Baker" type of *Solanum tuberosum* L., a carpellate cone of *Pseudotsuga taxifolia* (Lam.) Britt., or a twig of an oak. These all have either two or three clockwise primary spirals and two or three counter-clockwise primary spirals. The *Populus* or the *Rubus* will show a prominent 5-angled pith and five ridges on the surface of the stem corresponding to the five vertical ranks of leaves. The numerical formula will thus be 2-3-5-1 or 3-2-5-1. The spiral system that has the clockwise primary spirals smaller in number than the counter-clockwise primary spirals is said to be a right-handed system and one that has the clockwise primary spirals larger in number than the counter-clockwise primary spirals is said to be a left-handed system. Since the vertical ranks curve in the same direction as the smaller number of primary spirals, the "right-handedness" or "left-handedness" of the system can also be determined by observing the spiral direction of the ranks whenever the curvature in these shows distinctly. Clockwise spiral ranks indicate a right-handed system, counter-clockwise spiral ranks indicate a left-handed system. The curvature, or degree of pitch, of the spiral in the ranks usually depends on the size of the ratio of difference



between the clockwise and counter-clockwise primary spirals, unless there is a distinct torsion of the entire system. The ranks, or radii, are always equal to the sum of the clockwise and counter-clockwise primary spirals with one characteristic exception. The secondary spirals are equal to the difference between the clockwise and counter-clockwise primary spirals and will curve in the same direction as the larger number of primary spirals. If the primary spirals are equal in number the difference will, of course, be zero, which indicates, as intimated above, that there are no secondary spirals but that the secondary system, with one exception, is cyclic.

In determining the primary spirals, always take the next higher, often partly overlapping leaf or other organ beyond the first by moving radially and vertically from the first to the second. Care must be taken, especially if internodes are present, that the primary spiral is not confused with a secondary. With a little practice the primary spirals can be determined without difficulty, especially if one uses a string or marks the successive units as the spiral is traced out.

To construct the projection diagram of the given right-handed system, with the formula 2-3-5-1, one proceeds as follows (fig. 1):

Draw a series of circles, suitably spaced, with pencil so that these guiding lines may be erased, if desired, after the diagram is completed. In figure 1 they have been drawn in ink for distinct reproduction. In a complex multispiral system the circles must be close together in order that a sufficient sample of the system may be shown. Next, draw the required number of radii, properly spaced, and correct these to indicate the spiral pitch of the ranks. These need not be measured accurately for ordinary purposes, since the essential nature of the system will be evident from the primary spirals to be drawn. The radii may be numbered with Roman numerals, always in a clockwise direction for the sake of simplicity and uniformity and always beginning with the uppermost one, as shown in figures 1, 10, 14, 15, 16, and 20.

Now to locate the positions of the members making up the spiral system, taking figure 1 as a model, begin with the upper radius, numbered I, and place a dot on the intersection with the first circle on the outside. Beginning with this point, count the circles or intersections on the radius, —1, 2, 3, 4, 5, 1,—placing a dot on the last “1” and so proceed until the available circles have been counted. To locate the positions on the second radius, pass from the top position on the first radius along the outermost circle, in a clockwise direction, to the second radius (II), and count the number of the clockwise spirals on this, namely,—1, 2, 1,—and place a dot on the second 1; then as before, beginning with this position, count the

intersections toward the center,—1, 2, 3, 4, 5, 1,—marking the second “1” and so proceed until the available intersections have been counted. From any dot on this second radius pass to the third radius (III) and as before count,—1, 2, 1,—again marking the second “1.” From this position then one can count the fives either toward the center or the circumference until the proper positions are all marked. One proceeds thus until the proper positions are all marked on all the radii. In case one wishes to proceed in a counter-clockwise direction from the starting point one must count the number of the counter-clockwise primary spirals to get the first position on the radius (V), namely—1, 2, 3, 1,—as will be evident by an inspection of figure 1.

After all the positions have been marked, the clockwise and counter-clockwise primary spirals may be drawn thru them. It is best to draw the spirals first with a pencil and then trace them in ink. In order to have a uniform system of graphs, the writer always represents the clockwise primary spirals with continuous lines, the counter-clockwise primary spirals with broken lines, the radii with lines of small dots, and the secondary spirals, not shown in figure 1, with lines of large dots. The clockwise primary spirals may be numbered with Arabic numerals and the counter-clockwise primary spirals with Arabic numerals in parentheses as in figures 1, 10, 16, and 21. Right-handed spiral systems are represented by figures 1, 2, 3, 4, 6, 7, and 15, and left-handed systems by figures 5, 8, and 20. Apparently all spiral systems may develop, by the law of chance, as right-handed or left-handed systems on branches of the same or of different plants.

Projection diagrams of spiral systems may, of course, be constructed without drawing guiding circles by simply drawing the proper radii and measuring off the given positions with a ruler, but this method is more apt to lead to mistakes in determining the proper positions.

#### SECONDARY SPIRALS AND CYCLES

A study of the spiral systems clearly indicates that no single “genetic spiral” can be used conveniently to analyze the numerous spiral systems developed in the vascular plants, since the secondary spirals can be one up to a large number. After the primary system has been constructed, secondary spirals are often clearly in evidence and they are sometimes easily seen on the plant itself (see figs. 3, 4, 6, 7, and 8, in which the secondaries are represented). The secondary spirals are determined by skipping one rank or radius when passing from one position to the next and as stated above they curve in the direction of the larger number of primary spirals, when proceeding from the circumference to the center,

or in the direction of the smaller number of primaries if one begins in the center. When the numbers of the primary spirals are large and the number of the secondary spirals is small, as one, two, or three, much counting can be saved in constructing the projection diagrams by determining the positions for the secondary spirals after the fundamental positions have been located on a single radius. If there is but one secondary spiral, as in figures 6 and 8, there will be but one-interval difference from one position to the next on the third radius as one proceeds, if there are two secondaries, as in figure 7, there will be a two-interval difference on the third radius, etc. If the system is cyclic the fact will be indicated by the fourth number of the spiral formula being a zero and the ranks will be parallel to the axis of the shoot unless there is a general torsion of the whole system. In the culmination type of the alternate two-ranked system, 1-1-2-0, there is an apparent exception to the rule that a zero in the fourth number indicates a cyclic system, but since such a system has come to unity, the zero may be interpreted as a cycle with but one member which has attained the highest efficiency of the correlative interaction, controlling the entire cross-section of the bud at the given level (fig. 16).

All types of cyclic systems can be represented by the same construction method as is used for the spiral systems with secondary spirals, but a simpler method is available, since by placing the positions alternately at the intersections of successive circles and radii, a similar projection diagram will be obtained. This method has long been used in representing the cyclic-spiral systems as represented by the common cyclic flowers of the Angiospermae. It may also be advantageously used for the diagrams of the cones of *Equisetum* and for some of the individual cones of *Zamia*, etc. When one considers the problem as a whole, it becomes evident that the cyclic systems are only special cases of the fundamental spiral system. Typical cyclic systems are represented by figures 11, 13, 19, and 21.

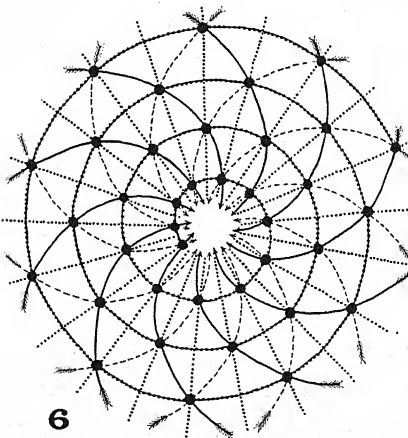
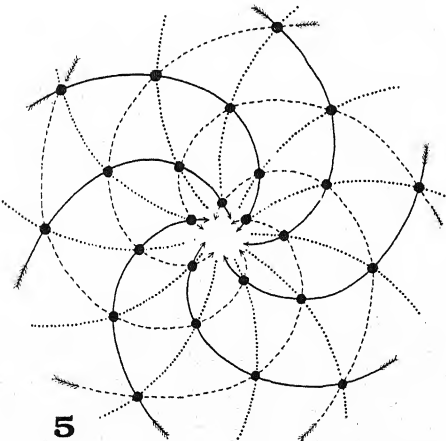
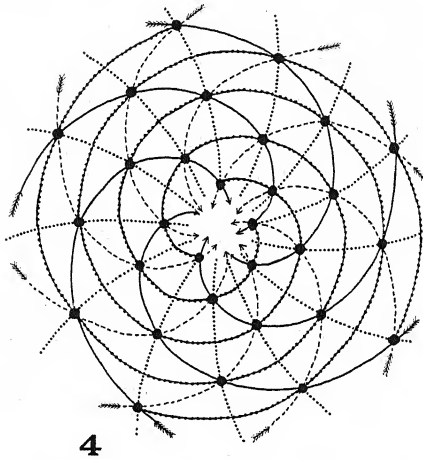
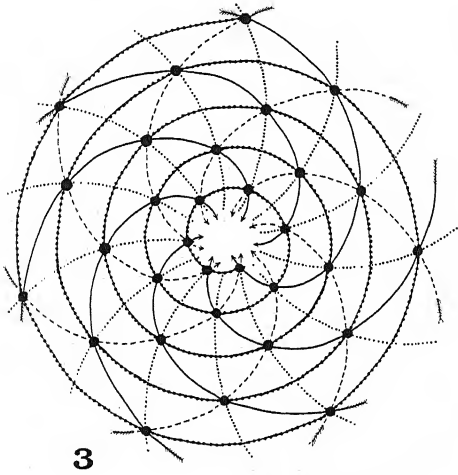
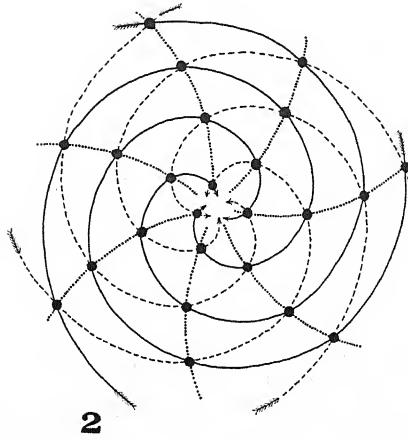
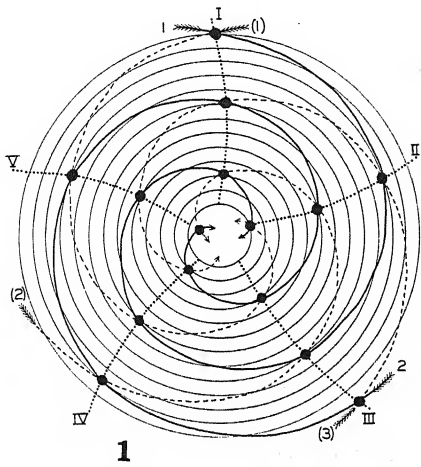
#### EXAMPLES OF REPRESENTATIVE SPIRAL SYSTEMS

In general, as stated above, the more primitive members of a phylogenetic series have variable spiral systems while advanced groups often have very stable systems, especially if they have attained one of the

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#### Explanation of Plate 22

- Fig. 1. Twig of *Populus balsamifera* L., spiral system 2-3-5-1.
- Fig. 2. Branch of *Lycopodium obscurum* L., 3-4-7-1.
- Fig. 3. Carpellate cone of *Zamia integrifolia* Ait., 6-7-13-1.
- Fig. 4. Carpellate cone of *Pinus caribaea* Mor., 5-8-13-3.
- Fig. 5. Carpellate cone of *Zamia integrifolia* Ait., 6-5-11-1.
- Fig. 6. Staminate cone of *Araucaria angustifolia* (Bert.) O. Ktz., 10-11-21-1.



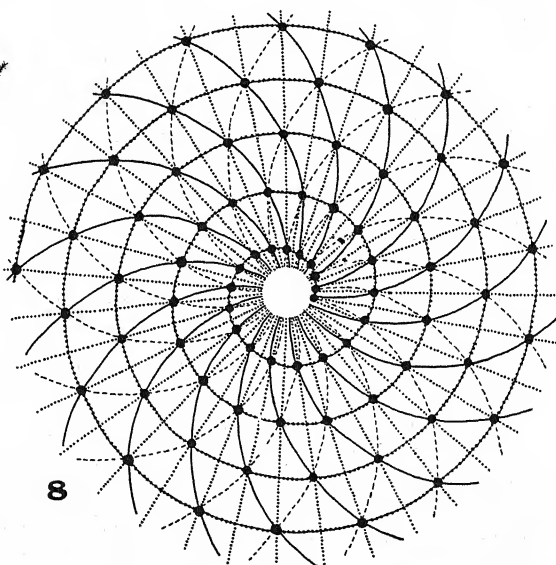
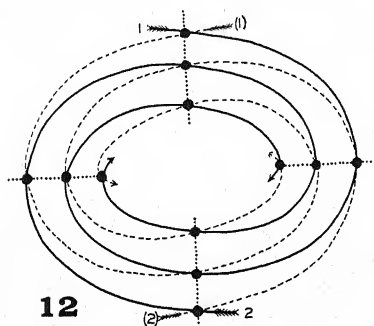
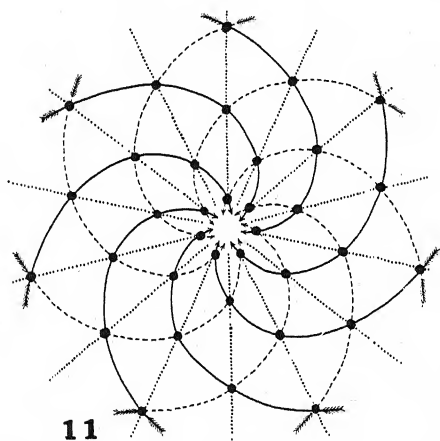
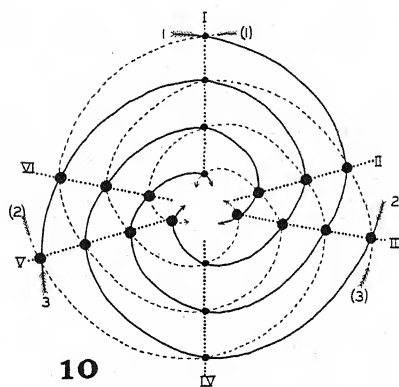
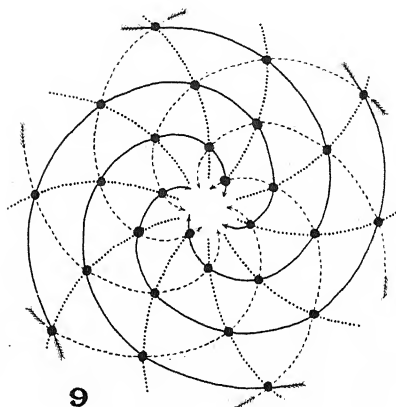
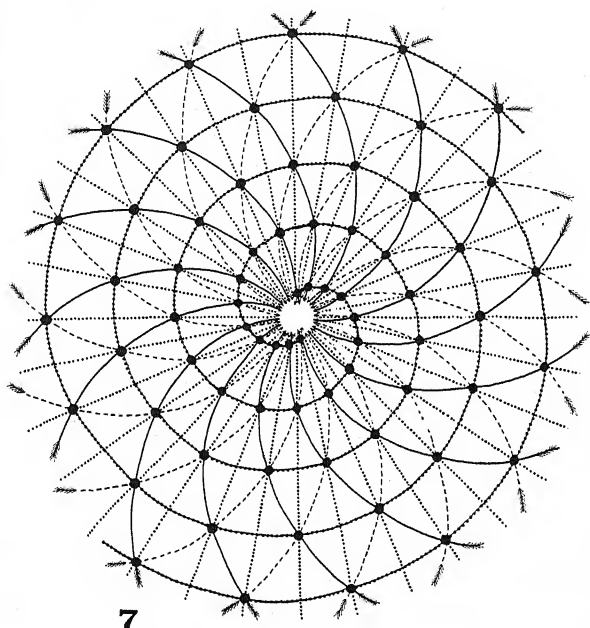
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several determinate culmination types of spiralization. If, however, an expansion hereditary factor has been added to the cell without a corresponding increase in the potentiality determining the control of an area around the incipient center from which a leaf is developed, then the spirals may again be decidedly increased and again show marked variability. *Lycopodium lucidulum* Mx. is one of the more primitive flowerless types of the living Lepidophyta. Its spiral system is commonly 4-5-9-1 or 5-4-9-1, or 4-4-8-0. Very often all three types are on different branches of the same plant. In the following examples only the formulae for right-handed systems are usually given, but it is to be understood that the corresponding left-handed systems of any given type are just as common either on the same plant or on different individuals. *Lycopodium annotinum* L. has the leaves in 4-5-9-1, 4-4-8-0, and 3-4-7-1 spiral systems and the same types for the sporophylls in the cones. In *Selaginella arenicola* Und. leaf spirals were noted of the formulae 4-4-8-0 and 3-4-7-1, and there are probably others present, while in the cones the sporophylls are reduced to the opposite 4-ranked arrangement, a 2-2-4-0 spiral system. In the numerous higher species of *Selaginella* both leaves and sporophylls are quite constantly of the opposite four-ranked type. In *Equisetum*, the lower species are exceedingly variable both in the leaf and sporophyll whorls, the number in a cycle varying with the size of the bud. In the most reduced species, *E. scirpoides* Mx., all cones and aerial stems constantly have trimerous whorls. The branches of *E. pratense* Ehrh. also, have trimerous whorls quite regularly. In one of the extreme water-ferns, *Azolla caroliniana* Willd., the leaf arrangement has attained one of the determinate limits, the alternate two-ranked condition, or 1-1-2-0 spiral system.

In various more advanced lines of vascular plants, the primary bud becomes very large without a corresponding increase in the evolution of the correlative interaction control and in consequence, as intimated above, the complexity of the spiral systems is greatly increased, as in species of *Cycas*, *Palmaceae*, *Yucca*, *Fourcroya*, *Cactaceae*, etc. A few stems of *Cycas revoluta* L. available for study had developed spiral systems as follows: 15-20-35-5, 18-21-39-3, 20-28-48-8, 21-34-55-13, and 34-21-55-13. A stami-

#### Explanation of Plate 23

- Fig. 7. Staminate cone of *Dioon edule* Lindl. (1936), spiral system, 15-17-32-2.
- Fig. 8. Staminate cone of *Dioon edule* Lindl. (1937), 18-17-31-1.
- Fig. 9. Branch of *Opuntia imbricata* (Haw.) Engelm., 4-6-10-2.
- Fig. 10. Dorsiventral branch of *Lycopodium obscurum* L., 3-3-6-0.
- Fig. 11. Staminate cone of *Zamia integrifolia* Ait., 7-7-14-0.
- Fig. 12. Flattened twig of *Libocedrus decurrens* Torr., 2-2-4-0





nate cone of the same species had the stamens arranged in a 14-17-31-3 spiral system. The staminate cones of *Dioon edule* Lind. usually vary on the same plant from one blooming season to the next. A staminate plant in the greenhouse had a cone in 1936 with the formula 15-17-32-2 (fig. 7), and in 1937 a cone with the formula 18-17-35-1 (fig. 8). A single carpellate cone available for study gave the formula 8-13-21-5 which corresponds to the Fabonacci fraction  $8/21$ . The new formula shows that the system is right-handed with five secondary spirals while the old Fabonacci fraction does not give this information directly. The flowers of *Zamia integrifolia* Ait. (*Z. floridana* DC.) are exceedingly variable and make a very good object for studying spiral systems. The following types of carpellate cones were found: 3-3-6-0, 4-4-8-0, 4-5-9-1, 5-5-10-0, 5-6-11-1, 6-5-11-1, 6-6-12-0, 6-7-13-1. Staminate cones studied gave the following formulae: 4-3-7-1, 5-5-10-0, 6-6-12-0, 6-7-13-1, 7-7-14-0. There are no doubt other types. Any complicated spiral system may for convenience be called a multispiral. A few carpellate cones of *Zamia furfuracea* Ait. were available for study. These had the following spiral systems: 3-5-8-2, 5-3-8-2, 4-4-8-0, 4-5-9-1, 6-5-11-1. A number of staminate cones of *Araucaria angustifolia* (Bert). Ktze. showed the following spiral formulae: 10-9-19-1, 10-10-20-0, 11-9-20-2, 10-11-21-1, 11-11-22-0, 11-12-23-1, 12-10-22-2, 12-11-23-1, and 12-12-24-0. The carpellate cones of many pines have the 5-8-13-3 spiral system, among which may be mentioned *Pinus caribaea* Mor., *P. taeda* L., *P. torreyana* Carr., *P. sabiniana* Dougl., *P. coulteri* D. Don., *P. nigra* Arnold, *P. virginiana* Mill., and *P. glabra* Walt. *Picea abies* (L.) Karst. also has carpellate cones with the 5-8-13-3 formula. Staminate cones of *Pinus nigra* Arnold vary considerably. Study of only a few cones gave the following spiral systems: 7-6-13-1, 7-7-14-0, 8-8-16-0, and 9-8-17-1. *Tsuga canadensis* (L.) Carr. usually has carpellate cones with a 2-3-5-1 or a 3-2-5-1 spiral arrangement but in a small collection one was found with a 4-3-7-1 system.

The alternate two-ranked spiral system, 1-1-2-0, is present in vegetative shoots of great numbers of the Angiospermae. This system, since it is a culmination reaction type, often shows a remarkable constancy, as in the four thousand species of grasses, most of the 10,000 to 15,000 species of Orchidaceae, the thousand species of the Iris family, most of the Scitaminales and numerous other Monocotylae. Large numbers of families and genera of Dicotylae have also attained this extreme, as for example *Asimina*, *Pedilanthus*, *Tilia*, *Cercis*, *Hamamelis*, *Ulmus*, *Celtis*, *Fagus*, *Planera*, *Ostrya*, *Betula*, etc. The opposite four-ranked system, 2-2-4-0, is also evolved in many families and genera. Occasionally this system may pass over in individual branches to a trimerous, cyclic condition, and

perhaps some trimerous genera and species are mutations from this type. Among the families with all or most of the species with opposite four-ranked leaves may be mentioned, Selaginellaceae, Juniperaceae, Gnetaceae, Oleaceae, Asclepiadaceae, Gentianaceae, Verbenaceae, Lamiaceae, Aceraceae, Aesculaceae, Hypericaceae, Dipsacaceae, Valerianaceae, Caprifoliaceae, and Caryophyllaceae. An abnormal system, apparently derived from the opposite four-ranked condition, is the opposite two-ranked spiral system, 2-2-2-0, in which the normal relation between the primary spirals and the number of ranks or radii does not hold. Two genera which have this extreme system are *Chamaesyce* and *Tribulus* (fig 18). It is interesting to note that in both genera the axillary buds or branches have a definite alternate two-ranked arrangement, only one of each pair of leaf axils producing a functional bud, which is alternate with the bud at the next node. Thus, we have here, in the same plant, both an alternate and an opposite position reaction. Another advanced type, but apparently not a culmination, is the spiral three-ranked condition, 1-2-3-1 spiral system, which is so prominently developed in the screw-palms, or Pandanaceae (fig. 15). This type is also very evident in the common greenhouse umbrella-plant, *Cyperus alternifolius* L., whose leaves, on a long reproductive scape, form three prominent clockwise or counter-clockwise spiral ranks. A common dicotyl genus with this leaf arrangement is *Alnus*.

In *Pandanus* the writer observed a bud sport in which the three-spiral changed suddenly to a straight, alternate two-ranked leaf arrangement and grew thus for five years, when it fell back just as suddenly to the normal, spiral three-ranked condition again (Schaffner 1919 and 1925). In this connection it is interesting to note that the two higher families of the Pandanales, Sparganiaceae and Typhaceae, have two-ranked leaves. The spiral ranks of *Pandanus* and the umbrella-plant are apparently not caused by a twisting of the tissues of the stem axis, but the torsion is due to the fact that of the two sets of primary spirals one is twice the number of the other. In *Rhoeo* and *Musa* the torsion of the two ranks apparently is due to a forward movement in the successive leaf positions produced by some factor influencing the interaction control system.

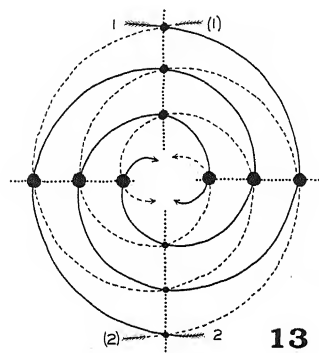
The most extreme and at the same time most puzzling spiral system is the unispiral, either clockwise, 1-0-0-0, or counter-clockwise, 0-1-0-0. Here the system is reduced to the ultimate limit of simplicity and altho the organization of the bud is apparently still radially symmetrical the reaction which produces the positions of the leaves is asymmetrical. A genus in which this type is present is *Costus*, as in *C. speciosus* (Koenig) Sm., belonging to the Zingiberaceae. This family normally has the alternate two-ranked spiral system. This unispiral of *Costus* has given rise to much

discussion and difference of opinion as to its cause. Apparently the condition is dependent on a definite hereditary factor for an inequilateral reaction in the growing bud. In the two highest families of the Scitaminales, Marantaceae and Cannaceae, the flowers, altho structurally radially symmetrical, are inequilateral in the development of their parts. A peculiar unispiral sometimes develops in the shoots of various species of *Equisetum*. Instead of the normal cyclic sheaths a spiral sheath may suddenly develop and usually after a time disappear just as suddenly, the shoot going back to the normal condition. Sometimes the ridges of one or more internodes above the spiral zone show a spiral twist or torsion (Schaffner 1927). In these cases there is apparently no addition of a new hereditary factor but simply a new reaction of the original heredity complex in the cells.

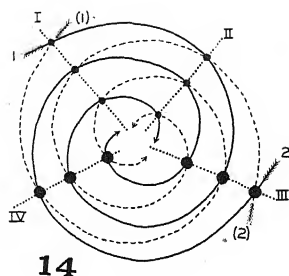
In the hypogynous Liliaceae, the lowest of the subclass Liliiflorae, one finds the *Aloe* group which contains a whole series of stages in the evolution of the spiral system from very complex multispirals to the normal determinate limit, the alternate two-ranked leaf arrangement. However, the early juvenile stage usually shows a very simple spiral system, even down to the alternate two-ranked condition, and only later is a more complex type developed. This is, of course, commonly the case in many groups, since it takes some considerable period of growth to develop the large-sized buds from which the multispirals develop. The writer has not had the opportunity to study any of the large tree species with complex spiral systems but among the species with complex multispirals are *Aloe rubrolutea* Schinz., *A. speciosa* Bak., and *A. aethiopica* (Schweinf.) Berg. The following species have been studied: *Haworthia reinwardtii* Haw., spiral formula 3-5-8-2; *Aloe arborescens* Mill., 2-3-5-1; *Kniphofia uvaria* (L.) Hook., 2-2-4-0; *Aloe variegata* L. and *A. viscosa* (L.) Haw., 1-2-3-1; *A. plicatilis* (L.) Mill., *A. haemanthifolia* Mar. and Berg., and *A. cooperi* Bak., 1-1-2-0; *A. ciliaris* Haw., 1-1-2T-0. The symbol T indicates a torsion system and that the ranks are definitely spiral where one would usually expect straight ranks.

#### Explanation of Plate 24

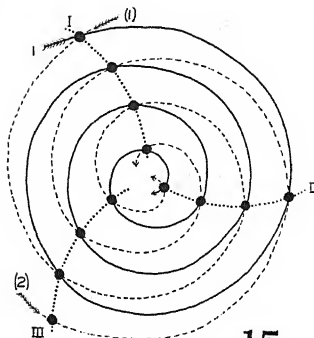
- Fig. 13. Dorsiventral branch of *Lycopodium complanatum* L., spiral system, 2-2-4-0.
- Fig. 14. Dorsiventral branch of *Selaginella kraussiana* A. Br., 2-2-4-0.
- Fig. 15. Inflorescence shoot of *Cyperus alternifolius* L., 1-2-3-1.
- Fig. 16. Twig of *Ulmus americana* L., 1-1-2-0.
- Fig. 17. Stem of *Rhoeo discolor* Hance, 1-1-2T-0.
- Fig. 18. Stem of *Chamaesyce preslii* (Guss.) Arth., 2-2-2-0.
- Fig. 19. Branch of *Lycopodium lucidulum* Mx., 4-4-8-0.
- Fig. 20. Sweet corn ear (6-rowed) of *Zea mays* L., 2-1-3-1.
- Fig. 21. Dent corn ear (24-rowed) of *Zea mays* L., 6-6-12-0.



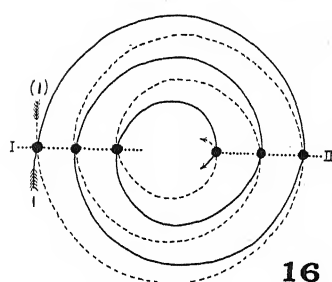
13



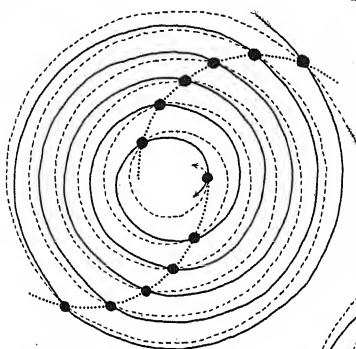
14



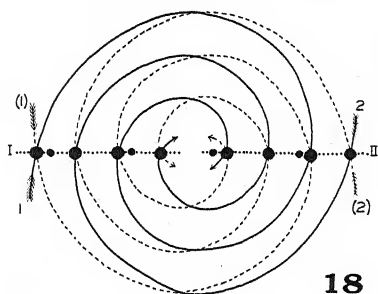
15



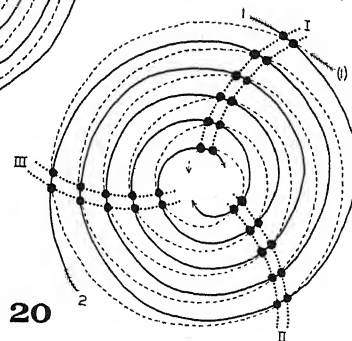
16



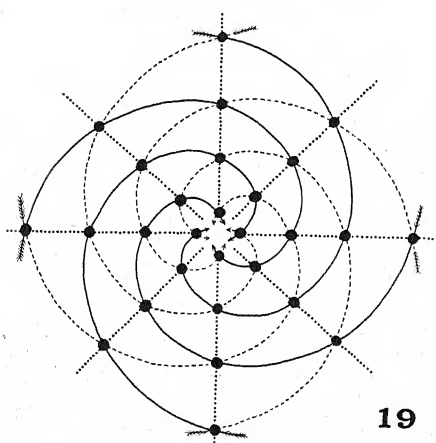
17



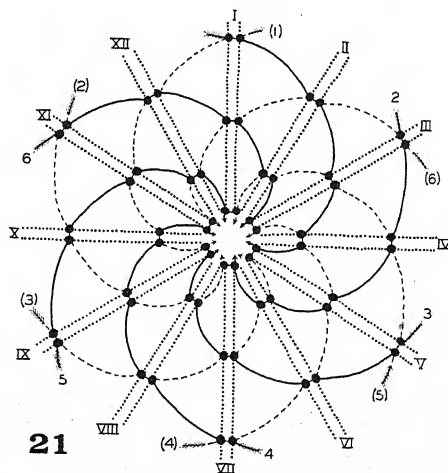
18



20



19



21

Variations in the spiral arrangement of the leaves is shown by the twigs of *Morus alba* L. The main axis, water shoots or vigorous branches may have a 2-3-5-1 arrangement or a 1-2-3-1 system and the more slender lateral twigs normally have the alternate two-ranked arrangement, 1-1-2-0. This condition apparently indicates that the white mulberry has attained the final potentiality of the two-ranked system but in such a weak condition that it is only expressed in the smaller, least vigorous buds. Similar conditions are frequently met in other groups. Thus in the oaks, *Quercus*, the leaves have the common five-ranked arrangement, 2-3-5-1, while in the chestnut, *Castanea dentata* (Marsh.) Borkh., the small lateral branches usually have the alternate two-ranked leaf arrangement while the more vigorous main branches have the 2-3-5-1 system. In the related beech, *Fagus americana* Sweet, the most advanced and specialized of the three genera, the branches usually have only the alternate two-ranked leaf arrangement. The juvenile arrangements do not, however, necessarily indicate the more primitive condition.

A plant which shows very prominently the relation between the primary spiral system and the vertical ranks is the common greenhouse species, *Euphorbia lacta* Haw. Very frequently one can observe among its various, thick, fleshy branches some with three spiral ridges, 1-2-3-1, some with four ridges, 2-2-4-0, and some with five ridges, 2-3-5-1. The primary spirals can easily be determined by twining strings around the stems thru the leaf positions or clusters of spines. The three-ranked joints usually show a decided, spiral twist.

#### EFFECT OF THE EVOLUTION OF SPECIAL EXPANSION FACTORS

Altho there is a general evolutionary movement in most advanced phylogenetic series toward a reduction and simplification of the spiral system, yet hereditary expansion factors are frequently introduced which may enlarge either the vegetative or reproductive buds and axes very decidedly and may thus cause a great increase in the number of spirals produced in the expanded part. With the introduction of such a factor, the hereditary reaction may again bring out decided fluctuations in the number of spirals produced. This condition is usually prominent in the disk of the common cultivated sunflower, *Helianthus annuus* L., and in the ear of Indian corn, *Zea mays* L. The great increase in the number of spirals in some stems of cacti has apparently also been caused by the evolution of expansion factors along with fleshiness.

The development of a great disk as in the common sunflower brings in a new mathematical problem, since there is a constant increase of the number of spirals on the disk from the center to the margin. In such a case



one can count the clockwise and counter-clockwise primary spirals at the outer part of the disk and simply write these two numbers in the formula. A disk  $4\frac{1}{2}$  inches in diameter had 55-86 primary spiral formula; one 11 inches in diameter had 83-122; one 15 inches in diameter had 144-89. It is evident that with a further enlargement of the disk, the number of the spirals could be much greater.

In the Andropogoneae, the spikelets are usually in pairs and thus if one wishes to ascertain the spiral arrangement in an ear of Indian corn, *Zea mays* L., a pair of grains must be taken for each position. The simplest ear has two double rows of grains and is thus a 1-1-2-0 spiral system. From this rare condition one can find, among the varieties, a continuous series up to the 6-6-12-0 (24-rowed) type and far beyond. The 6-rowed ear, 1-2-3-1 spiral system, is also exceedingly rare (fig. 20). A diagram of a 24-rowed ear is shown in fig. 21. A 14-rowed ear has a 3-4-7-1 or 4-3-7-1 spiral system. The ear often changes from a higher to a lower system at or near the middle. Thus an ear was found having 16 rows in the lower half and 12 in the upper half; another one had 20 rows in the lower half and 18 in the upper half. When the change is abrupt, as it was in these two cases, there is irregularity on the transition zone but the normal double-row, spiral system is soon established again with the reduced numbers.

#### EXAMPLES FOR A SYSTEMATIC STUDY OF THE SIMPLER SPIRAL SYSTEMS

In the list below only right-handed formulae are given. All those with unequal numbers of clockwise and counter-clockwise primaries will also occur in the left-handed condition.

- I. Examples of complex multispiral systems are represented by Figs. 6, 7, and 8.
- II. Cyclic spiral system 7-7-14-0, a staminate cone of *Zamia integrifolia* Ait. (fig. 11).
- III. Spiral system 6-7-13-1, a carpellate cone of *Zamia integrifolia* Ait. (fig. 3).
- IV. Spiral system 5-8-13-3, involucre of artichoke, *Cynara scolymus* L., inflorescence fruit of the pineapple, *Ananas comosus* (L.) Merrill, carpellate cone of *Pinus caribaea* Mor. (fig. 4).
- V. Cyclic spiral system 6-6-12-0, a carpellate cone of *Zamia integrifolia* Ait., vegetative shoots of *Galium triflorum* Mx. and *G. concinnum* T. & G.
- VI. Spiral system 5-6-11-1, a carpellate cone of *Zamia integrifolia* Ait.
- VII. Cyclic spiral system 5-5-10-0, a staminate cone of *Zamia integrifolia* Ait., a large stem of *Selaginella arenicola* Und. This is a pentamerous ten-ranked system.
- VIII. Spiral system 4-6-10-2, a branch of *Opuntia imbricata* (Haw.) Engelm. (fig. 9).
- IX. Spiral system 4-5-9-1, branches of *Lycopodium lucidulum* Mx. and *L. annotinum* L. and main stem of *L. obscurum* L.
- X. Cyclic spiral system 4-4-8-0, some branches of *Lycopodium lucidulum* Mx., some cones of *L. obscurum* L., some branches of *Equisetum arvense* L., some stems of *Selaginella arenicola* Und., stem of *Galium circaezans* Mx. This is a tetramerous, eight-ranked system (fig. 19).
- XI. Spiral system 3-5-8-2, carpellate cones of *Pinus strobus* L. and *Sequoia washingtoniana* (Winkl.) Sudw., branch of *Opuntia imbricata* (Haw.) Engelm.
- XII. Spiral system 3-4-7-1, some shoots of *Selaginella arenicola* Und., some cones of *Lycopodium obscurum* L., some branches of *Opuntia imbricata* (Haw.) Engelm. (fig. 2).



- XIII. Cyclic spiral system 3-3-6-0, *Equisetum scirpoides* Mx., *Salvinia natans* (L.) Hoffm., *Juniperus communis* L., some branches of *Catalpa speciosa* Ward., flowers of *Yucca*, *Lilium*, *Iris*, etc. This is a ternate six-ranked system (fig. 10).
- XIV. Spiral system 2-3-5-1, twigs of *Rhus glabra* L., young shoots of *Asparagus officinalis* L., *Quercus* sp., *Populus* sp. This is the five-ranked spiral system and is very common (fig. 1).
- XV. Cyclic spiral system 2-2-4-0, the higher species of *Selaginella*, *Thuja*, *Gnetum*, *Naias*, *Acer*, *Salvia*, *Bidens*, etc. This is the opposite, or dimerous, four-ranked system and is a very common culmination type (figs. 13, 14).
- XVI. Spiral system 1-2-3-1, *Pandanus* sp., *Alnus* sp., reproductive shoot of *Cyperus alternifolius* L. This is the alternate spiral three-ranked system (fig. 15).
- XVII. Cyclic spiral system 2-2-2-0 with the axillary buds and branches in the 1-1-2-0 spiral system, *Chamaesyce* sp., *Tribulus terrestris* L. This is the rare, abnormal, opposite two-ranked system (fig. 18).
- XVIII. Alternate two-ranked torsion system with the two ranks prominently spiral, 1-1-2(T)-0, *Cordyline terminalis* Kunth, *Rhoeo discolor* Hance, *Musa sapientum* L. (fig. 17).
- XIX. Spiral system 1-1-2-0, *Azolla*, *Graminaceae*, *Iridaceae*, *Asimina*, *Tilia*, *Cercis*, *Ulmus*, *Zygocactus truncatus* (Haw.) K. Schum. This is the normal alternate two-ranked arrangement with straight or nearly straight ranks and is the normal culmination type of the spiral system in many plant groups (fig. 16).
- XX. Unispiral system, 1-0-0-0 or 0-1-0-0, *Costus speciosus* (Koenig) Sm. and shoots or zones of shoots of *Equisetum* sp. This is a very rare abnormal type, showing an inhibition of the fundamental, radially symmetrical reaction system.

SUMMARY STATEMENT OF RELATIONS IN THE SPIRAL SYSTEMS AND  
METHODS OF CONSTRUCTING FORMULAE AND PROJECTION  
DIAGRAMS

1. All normal spiral systems, developed on a cylinder, have both clockwise and counter-clockwise primary spirals, the direction to be determined in the direction of growth. In constructing projection diagrams of spiral systems the base is always to be represented at the outer part of the circle and the upper part in the center.
2. If the number of clockwise primary spirals is smaller than the number of counter-clockwise primaries, the system is said to be right-handed and if the number of clockwise primary spirals is larger than the number of counter-clockwise primaries, the system is said to be left-handed.
3. The number of vertical ranks, or radii, is equal to the sum of the clockwise and counter-clockwise primary spirals, except in the rare, opposite two-ranked arrangement which is an abnormal type.
4. The vertical ranks, or radii, curve in the same direction as the smaller number of primary spirals. A right- or left-handed system can then also frequently be determined by the spiral direction of its vertical ranks. If the ranks curve in a clockwise direction the system is right-handed, if counter-clockwise, the system is left-handed.
5. The secondary spirals are equal in number to the difference between the clockwise and counter-clockwise primary spirals and are determined

by skipping one radius in going from one position to the next on the projection diagram or on the spiral cylinder.

6. The secondary spirals curve in the same direction as the larger number of primary spirals in the system.

7. If the clockwise and counter-clockwise primary spirals are equal in number, there are no secondary spirals but the parts are in cycles and the ranks, or radii, are straight and parallel to the axis unless there is torsion of the entire system. The cyclic condition is produced whenever the pitch of the clockwise and counter-clockwise spiral screws becomes equal. In the extreme, alternate two-ranked system, the rule that the zero indicates a cyclic system does not hold unless it is assumed that the one member controlling the entire cross-section of the growing bud at the given level makes a cycle.

8. Any spiral system can be conveniently represented by a formula of four numbers as, for example, the common, right-handed, five-ranked type by 2-3-5-1, or the opposite four-ranked type by 2-2-4-0. The first number represents the clockwise primary spirals, the second number the counter-clockwise primary spirals, the third number the ranks, or radii, and the fourth number the secondary spirals, or if the number is zero a cyclic system without any secondary spirals.

9. The two possible, normal evolutionary culmination types are the opposite four-ranked and the alternate two-ranked systems, both of which are very abundant in the higher evolutionary levels of certain phyletic lines.

10. The two abnormal culmination types, which form exceptions to the general rules of spiralization are the opposite two-ranked and the unispiral conditions, in both of which there is some exceptional factor which changes the normally, radially symmetrical reaction of the growing stem bud.

11. Any spiral type may be distorted by growth torsion or by twisting of the whole system.

12. Irregularities in positions may be developed in any system during growth when the reaction changes from one type to another thru the influence of internal or external environmental conditions, especially when the cell system contains factors for more than one type of reaction, as in those plants which have potentialities for both the primary-secondary spiral system and the primary spiral-cyclic system. Certain abnormal developments, as faciation for example, may cause very great disturbances, but these abnormalities have no direct bearing on the problem of the fundamental nature of the spiral systems.

## HISTORICAL DEVELOPMENT AND BIBLIOGRAPHY OF SOME RECENT PAPERS

Consideration of the historical development of the theories of phyllotaxy may properly begin with Bonnet, who published a paper on the subject in 1754. Later, in the years 1830-1835, Schimper and Braun elaborated a system of phyllotaxy and their treatment became the common basis for both criticism and further theory. In the meantime, many investigators, both before and after Schimper and Braun, considered the subject, among whom may be mentioned Goethe, the brothers Bravais, Wiesner, Hofmeister, Schwendener, Eichler, C. de Candolle, and Warming.

Below is given a partial list of important references to the literature which has appeared since the beginning of the present century. However, there are many other papers of importance, besides the ones mentioned, which may be studied by those who are interested in the recent treatment of the subject and the theoretical views entertained.

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# Structure and Growth of the Shoot Apex in *Ginkgo Biloba*

ADRIANCE S. FOSTER

(WITH 12 FIGURES AND PLATES 25 TO 27)

## INTRODUCTION

Although an extensive literature has developed regarding the morphology and phylogenetic relationship of *Ginkgo*, cf. bibliography in Sprecher (1907), Seward and Gowan (1900), Chamberlain (1935), no careful investigation seems to have been made of the structure of the shoot apex of this primitive gymnosperm. In the meagre literature devoted to this aspect of *Ginkgo*, two opposed interpretations have appeared. Strasburger (1872 p. 327) concluded that the growing point is differentiated into three well-defined histogens, viz.: an independent "protoderm," a two-layered periblem and a central plerome. Fankhauser (1882, p. 4) confirmed this interpretation with the qualification that the limits between the periblem and plerome are not always distinct. In contrast, Solms Laubach (1884, p. 154, Plate XVIII, fig. 2) described and figured in surface view, a large apical cell with definite segments, in the shoot apex of the seedling. The observations of Sprecher (1907, p. 15), at least in respect to the embryo, failed to support either of these views. Sprecher found that periclinal divisions occur in the superficial layer (i.e. Strasburger's "protoderm") and that furthermore the periblem and plerome arise from a common group of initials. Unfortunately, Sprecher did not investigate the structure of the growing point of the buds of spur and long shoots of the tree.

The evident need for a thorough study of the organization and growth of the shoot apex of *Ginkgo* prompted the present study. In addition, it was hoped that information on this primitive gymnosperm might throw some light upon the disputed organization of the growing point in the Coniferales<sup>1</sup> and hence might lead to a better understanding of the evolution of the apical meristem in seed plants.

It is a pleasure to express my thanks to my wife for her invaluable assistance in the preparation of the illustrations used in this paper. I am also appreciative of the help given by Dr. Otto Schüëpp of Basle with several difficult points of theory. Acknowledgement is made for the grant furnished by the Board of Research of the University of California.

## MATERIALS AND METHODS

The material used in the present investigation was obtained from several large microsporangiate trees growing near and on the campus of

<sup>1</sup> For reviews of the literature cf. Koch (1891), Schüëpp (1926), Korody (1937).



the University of California, Berkeley. During April, May and early June of 1937 terminal buds of vigorous spur shoots were collected two or three times a week. Additional bud material of both spur and long shoots was secured late in the dormant period as well as during the period of shoot elongation in 1938.

To facilitate the rapid penetration of the formalin-acetic acid-alcohol solution used as a killing and fixing reagent, the outer foliar organs were first removed from the buds and the shoot apices then gently evacuated in the killing fluid. The material was dehydrated, cleared in xylene and embedded in paraffin by the usual technique. Serial longitudinal and transverse sections were cut at a thickness of 6, 7 or 8 microns and stained with tannic acid and iron chloride in conjunction with safranin (cf. Foster, 1934). Since accurate orientation of the shoot apices on the block-carrier of the microtome is impossible, it was necessary to section numerous buds in order to secure a significant number of "median" series. The information presented in this paper is based upon a detailed study of nearly 100 longitudinal and about 50 transverse series.

The drawings in this article were prepared as follows: the sections chosen for illustrations were photographed using a high dry objective. Prints were then made on "mat" paper upon which the desired cell outlines and contents were lightly traced in pencil. The final step consisted in placing the prints in a solution which removed the photographic image, after which the penciled outlines were retraced in ink. Unless otherwise stated, all text figures represent a magnification of  $\times 17.5$  diameters. The photomicrographs with the exception of text figs. 1 and 2 were taken under oil immersion and have not been reduced for reproduction.

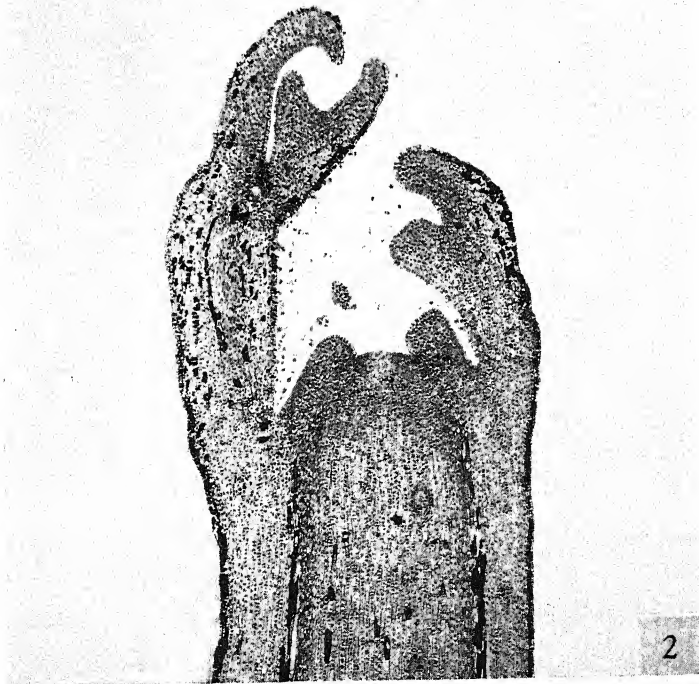
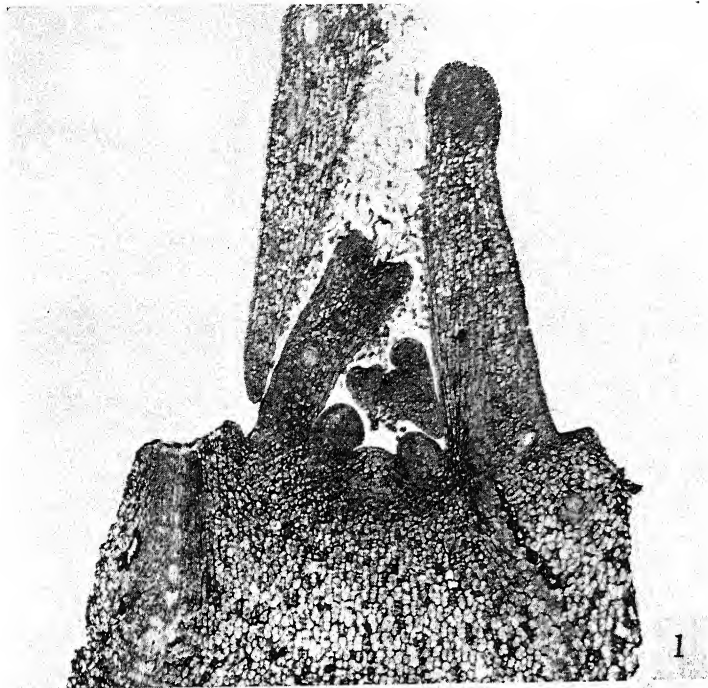
#### GENERAL MORPHOLOGY AND PERIODICITY OF THE SHOOT SYSTEM

Before describing the structure and growth of the shoot apex, it will be necessary to note briefly certain features of the morphology and periodic development of the vegetative shoot system. As is well known, two well-

#### Explanation of Figures 1-2

Fig. 1. Median longisection of the upper portion of a spur shoot, April 15, showing the meristematic apex between the two youngest bud-scale primordia. Note the zone of lightly-stained central mother cells, the absence of distinct internodes and the abrupt transition from the rib meristem to the broad expanding pith.  $\times 35$ . (The detailed structure of the apex of this shoot is shown on Plate 25, fig. 1.)

Fig. 2. Longisection of the upper portion of a long shoot April 18, showing the meristematic apex between the two youngest foliage-leaf primordia. Contrast the prominence of the rib meristem in the future pith and cortical regions and the consequent formation of distinct internodes with the condition in the spur shoot in Fig. 1. Two secretory cavities are seen developing in the central region of the rib meristem.  $\times 35$ . (The detailed structure of the apex of this shoot is shown on Plate 27, fig. 1.)



Figures 1-2

defined types of shoots occur in *Ginkgo*, viz.: long shoots, characterized by elongated internodes and relatively small pith and cortex and spur or dwarf shoots, with much abbreviated internodes and comparatively large pith and cortical regions. Observation shows however that these two types of shoots are not morphologically "fixed" in character since the terminal bud of a spur shoot may give rise to a long shoot, and conversely the apical bud of a long shoot may fail to form extended internodes, thereby producing a dwarf shoot (cf. Doak 1935 p. 46, fig. 24). Examination of the trees used in this study indicated that while the "lateral" spur shoots may exhibit a similar growth rhythm for many successive years, a "terminal" spur shoot is very often followed the next season by a true long shoot. The physiological aspects of the mutability and periodicity of spur and long shoots in *Ginkgo* clearly deserve investigation.

From an histogenetic standpoint, it is significant that no fundamental difference has been found in the cellular organization of the growing points in the two types of shoots. As is shown clearly in Figures 1 and 2, the differences seem to lie basically in the relative extent of and duration of activity in the rib meristem of cortex and pith regions. In the spur shoot, the vertical extent of the rib meristem is short and is followed abruptly by the region of expanding and maturing parenchyma; internodal elongation consequently is at a minimum. In contrast, the production of a long shoot is always associated with a prolonged period of cell division and cell elongation in the rib meristem and the inevitable formation of well-defined internodes.

As is true of many gymnosperms (Koch 1891, Korody 1937) shoot development in *Ginkgo* involves the annual formation of a series of cataphylls followed by the production of foliage leaves. However, unlike the situation in *Abies* described by Korody (1937 p. 29) there is little appreciable difference in the relative size or shape of the growing point in *Ginkgo* during the scale and foliage-leaf forming periods (figs. 1 and 2). Although no attempt has been made in this study to contrast the developmental history of cataphyll and foliage leaf, a brief description will be given later of the early phases in the initiation of these organs.

#### THE ZONAL STRUCTURE OF THE SHOOT APEX

The most distinctive feature of the meristem of the shoot apex<sup>2</sup> of *Ginkgo* is the segregation of its cells into a number of well-defined zones. Fig. 3 represents an effort to depict schematically the position and direc-

<sup>2</sup> Throughout the present paper, the entire apical region of a bud will be designated as the "shoot apex." The more restricted term "growing point" has such a vague and ambiguous connotation that its use will be avoided as far as possible.

tions of growth of the cells in each zone. Without doubt, Zone II is the most distinctive and unique structural region of the growing point. When viewed in median longisection, this zone appears as a prominent cup-shaped group of large, polygonal, lightly-stained cells which are situated in the upper median region of the shoot apex (cf. Plates 25 and 27). From a careful observation of many "median" series it is evident that *cell enlargement*, rather than cell division is the dominant process characteristic of Zone II. As a consequence, this zone always remains clearly demarcated from the remaining tissue of the growing point, which is composed of much smaller and more frequently dividing cells. The region of transition

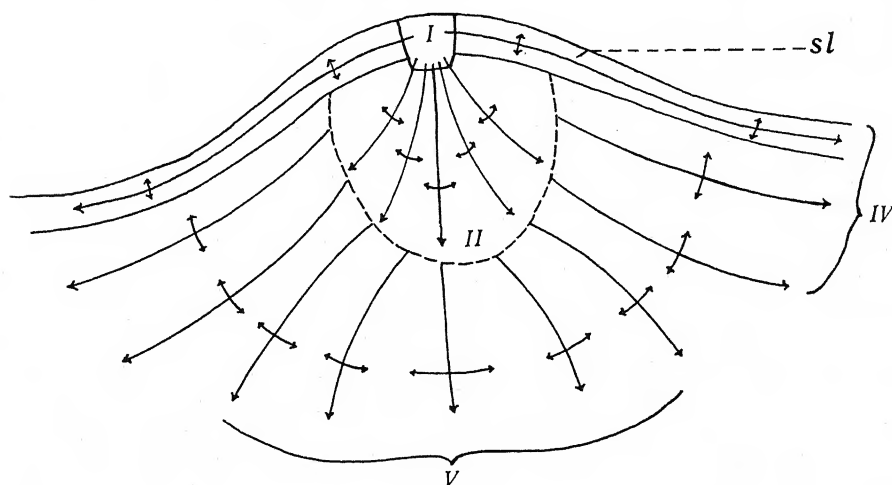


Fig. 3. Diagram illustrating the zones and their mode of growth in the shoot apex of *Ginkgo*. Zone I represents the position of the *apical initial group*, from which by anticlinal and periclinal divisions respectively the surface layer (sl) and the internal tissue of the growing point originate. Zone II is the prominent cup-shaped mass of large, slowly dividing *central mother cells*. As indicated by the arrows, volume growth predominates in this zone. The lateral and basal margins of the group of central mother cells (indicated by the broken U-shaped outline) constitute Zone III, characterized by the smaller size and frequency of division of its cells. From this "transition" zone arise the peripheral subsurface layers (Zone IV) and the rib meristem (Zone V). The long arrows in the surface layer and in Zones IV and V indicate the prevailing directions of growth in respect to the surface of the growing point. In the surface layer and in Zones II, IV, and V, the small double arrows represent the relative amount of growth at right angles to the prevailing direction.

from Zone II to Zones IV and V, as seen in longitudinal view, consists of a U-shaped zone of small, tabular cells; from the latter radiate the densely cytoplasmic inner peripheral layers (Zone IV) and the filamentous cell groups of the rib meristem (Zone V). In transverse sectional view, the

U-shaped "zone of transition" appears as a cylinder of cambial-like cells which entirely surround the cells of Zone II (Plate 26, figs. 1, 2). Since Zone II clearly functions as the common point of propagation of most of the internal tissue of the growing point, its component cells will be termed "central mother cells." Nevertheless, it must be emphasized that the *ultimate* source of all cells in the shoot apex of *Ginkgo* is represented by the *apical initial group* (Zone I, fig. 3; figs. 4, 5, 6c, 7a, 11, 12). These surface cells occupy the median apical region of the growing point and by means of anticlinal and periclinal divisions add new cells respectively to the surface layer (sl in all text figures) and to the central mother cells. However, as will be shown later, the behavior of the cells of the apical initial group seems entirely subordinated to the *growth of the shoot apex as a whole* and in no sense is comparable to the orderly and precise segmentation typical of certain vascular cryptogams. With this general account of the organization and growth of the shoot apex of *Ginkgo*, a more detailed description can be given now of the various zones.

#### APICAL INITIAL GROUP (Zone I, fig. 3)

At the outset, it may be stated that no evidence has been found of the existence of a single permanent apical cell. The presence of such a cell in the shoot apex of the seedling, as described by Solms-Laubach (1884) seems very questionable, particularly since his observations were confined to a surface view of the growing point. Furthermore Lyon (1904 p. 278) in his careful embryological study of *Ginkgo* emphasized that shoot and root growing points "arise through a localization of growth activity out of one general meristematic tissue; and hence from the first are many-celled meristems."

Because of the broad and only slightly elevated form of the growing point, perfect transverse sections of the surface were only rarely obtained in the present study. Figure 4 represents an approximately transverse section through the surface layer and shows a central group of four prominent cells which doubtless represent initials. It is obvious from this preparation, as well as from serial longisections, however, that no regular plan of segmentation exists. New anticlinal and periclinal division walls are inserted at varying angles and frequencies and only rarely is it possible to trace a whole series of surface or internal cells to the repeated division of any of the initials. In other words the geometrical apex of the shoot is occupied by a group of cells, variable in number, from which all the remaining tissue originates. Using Schüepp's (1926 p. 45) terminology, these initiating cells will be designated collectively as the "apical initial group." In their general mode of growth and variable sequence of cleavage, the



cells of the apical initial group in *Ginkgo* are fundamentally similar to the single tier of initials characteristic of *Abies*, *Picea* and *Pinus* (Korody 1937) and of various species of *Lycopodium* (Härtel 1938).

A comparison of serial longisections through many shoot apices in *Ginkgo* demonstrates that while anticlinal, periclinal and periclinal-oblique divisions occur in the apical initial group, there is no regular sequence in these planes of cleavage. According to the recent investigations of Härtel (1938), anticlinal divisions predominate over periclinal divisions in the apical initial group in the shoot apex of *Lycopodium*. Whether a similar condition occurs in *Ginkgo* is not apparent from the present study. It is conceivable however, that significant differences in respect to the relative

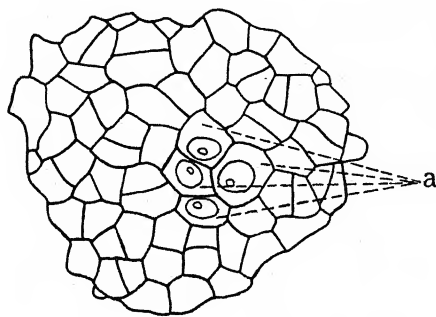


Fig. 4. Surface view of the apex of a spur shoot showing a central group of apical initials (a) and the irregular arrangement of the surface cells derived from them.

frequency of periclinal and anticlinal divisions might be detected in a statistical comparison of long and spur shoots. Some preparations of spur shoots indicate that anticlinal divisions have dominated for a time resulting in the propagation of a regular series of surface cells (figs. 8, 9, 10). Very frequently however, one or more cells in the apical initial group enlarge in an anticlinal direction and then divide by strictly periclinal or periclinal-oblique walls (figs. 5, 6a, 7a, 11, 12; Plate 25, fig. 2; Plate 27, fig. 2). The behavior of the daughter cells resulting from such divisions is highly variable. Often, each cell divides anticlinally resulting in a group of four cells, the outer two of which continue to function as initials while the inner two become incorporated in the zone of central mother cells (fig. 7a). In some instances, this "decussate" type of division may occur in several adjacent cells. Figure 11 for example reveals the products of a trio of unusually prominent apical initials, the laterals of which have divided in a decussate manner while the median cell pair is preparing for the anticlinal division. In other preparations however, the interpretation of the cell net in the apical initial group is complicated by (1) the irregular



sequence of anticlinal and periclinal divisions and (2) the wall-bending and enlargement of the inner segments (figs. 6b, 6c, 12). Similar difficulties have been encountered by Härtel (1938 p. 141, figs. 16-19) in the shoot apex of *Lycopodium*.

Lastly it must be noted that, as is true of many conifers (Koch 1891, Korody 1937) and *Lycopodium* (Härtel 1938), periclinal divisions are not confined to the apical initial group in *Ginkgo* but may occur at any point in the surface layer (figs. 6c, 6d, 7b, 10; Plate 25, figs. 1, 2; Plate

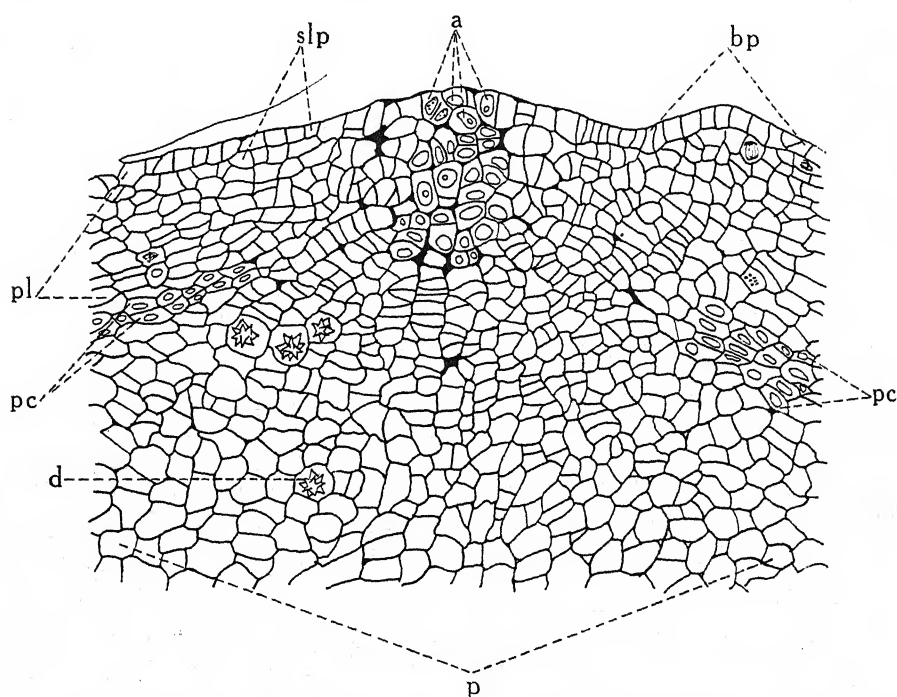


Fig. 5. Median longisection of the tip of a spur shoot, illustrating the typical segregation of the meristem into well-defined zones.  $\times 161$ . In this and all following figures, the extent of the zone of central mother cells is represented by the large nucleated cells and localized "wall-thickenings" are shown by heavy black outlines.

Legend for all figures: *a*, cells of the apical initial group; *bp*, primordium of bud scale; *d*, druse; *p*, pith; *pc*, procambium, *pl*, zone of peripheral layers; *r*, zone of rib meristem; *slp*, periclinal division of surface layer.

27, figs. 1, 2). Consequently, as represented by the small double arrows in Figure 3, the surface layer cannot be regarded as a "dermatogen" (Hanstein 1868) or "protoderm" (Strasburger 1872, footnote p. 325) but on the contrary represents the point of origin of a variable portion of Zone IV. From a cytological standpoint, it is interesting to note that in contrast to the slightly larger and more lightly-stained cells of the apical initial group, the surface cells on the flanks of the apex are smaller and stain

more deeply with safranin (Plate 25, figs. 1, 2; Plate 27, figs. 1, 2). In this respect, they are identical with the cells of the inner peripheral layers and hence are regarded as an integral part of Zone IV (cf. fig. 3).

CENTRAL MOTHER CELLS (*Zone II*, fig. 3)

In spite of their position in the upper central region of the shoot apex, the central mother cells have none of the characteristics usually associated with the primordial meristem of seed plants (Priestley 1928, 1929). In the first place, they are the largest cells of the apical meristem, often reaching a maximum length of 30–35 microns and a width of 15–20 microns; the cells of the peripheral layers and of the “transition zone” in contrast average  $\frac{1}{2}$  to  $\frac{1}{3}$  these dimensions. The “enucleated” appearance of certain of the central mother cells shown in Plate 26, figs. 1 and 2 illustrates how, in such large cells, the plane of a thin section may be above or below the level of the nucleus. Secondly, the central mother cells are sharply demarcated from the neighboring peripheral layers (Zone IV) by their larger, more lightly stained nuclei and by the less dense and more vacuolated appearance of their cytoplasm (Plates 25–27). Indeed, from a purely cytological standpoint, the zone of central mother cells bears a marked resemblance to the young apical-cell segments typical of certain vascular cryptogams (Kaplan 1937 p. 229, Zirkle 1932 p. 32). Admittedly, however, the present study is limited to a description of appearances obtained when meristem is killed and fixed in formalin-acetic acid-alcohol and stained in safranin. A further study of the whole problem therefore with the use of a wide range of killing reagents (Zirkle 1932) and stains (Vidal 1912), would certainly be profitable.

Although mitoses have been observed in the central mother cells (figs. 7b, 8, 9; Plate 26, fig. 1; Plate 27, fig. 2) they are noticeably less frequent than is true of the cells of Zones IV and V. Furthermore, indirect evidence of the reduced mitotic activity of the central mother cells is furnished by their relatively large size and by the lightly stained appearance of their nuclei. These facts suggest that, unlike the situation in the primordial meristem of angiosperms, cell enlargement rather than cell division is the dominant aspect of growth in the central mother cells.

As indicated by the highly irregular arrangement of cells, *growth in volume* is typical of the zone of central mother cells, which thus agrees, at least in this respect, with the corpus region of the angiospermous growing point.<sup>3</sup> A careful examination of longitudinal and transverse series shows that no regular plan of segmentation is followed by the central

<sup>3</sup> For details regarding the tunica-corporis zones of the shoot apex in angiosperms cf. Schmidt (1924), Priestley (1928, 1929), Foster (1935, 1936, 1937), Cross (1936, 1937, 1938), Newman (1936), Kliem (1937).

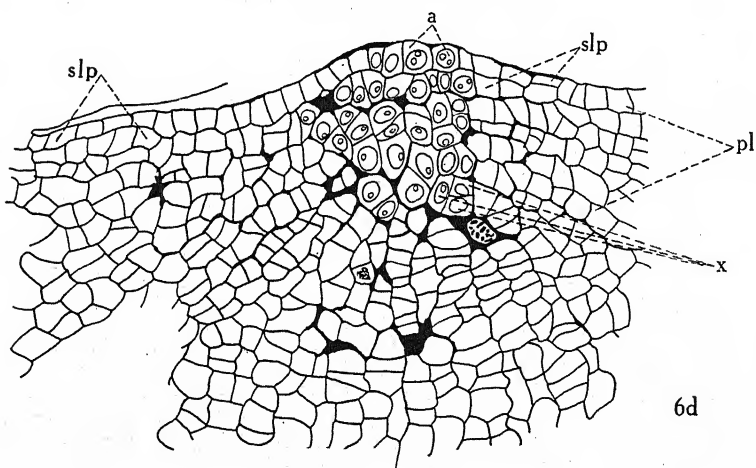
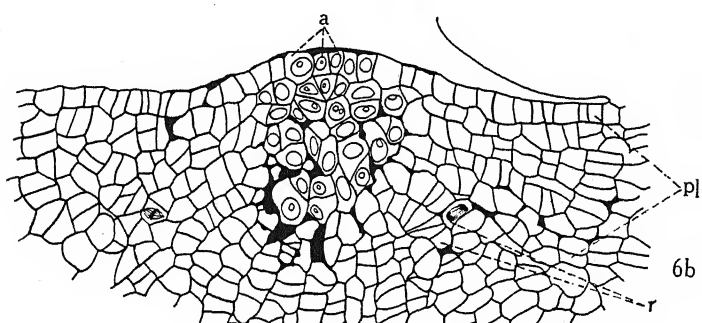
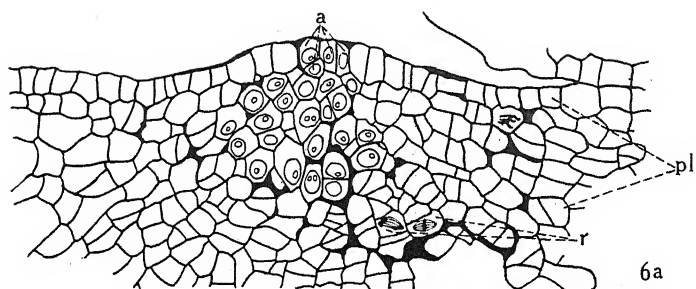
mother cells. Nevertheless, there is a marked tendency for the cells, especially in the "axial" region, to divide periclinally in respect to the surface of the shoot apex (figs. 6b, 6c, 6d, 8, 9, 12; Plate 25, fig. 1; Plate 27, figs. 1, 2). Following such divisions, either or both of the daughter cells may divide anticlinally (figs. 6c, 6d, 7a, 10, 11; Plate 27, figs. 1, 2). In this way, new cells are continually formed toward the peripheral and basal regions of the zone. However, the wall-bending and unequal enlargement of all cells, as well as frequent obliquities in the insertion of new walls are facts which preclude any exact determination of cell lineages. Consequently, it seems reasonable to conclude that fluctuations in the rate and directions of growth within the "plastic" mass of central mother cells determine the cell pattern at any given point, rather than any inherent sequence of cleavages.

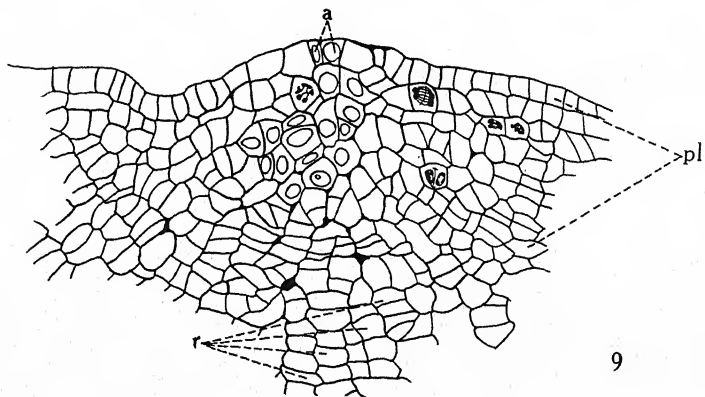
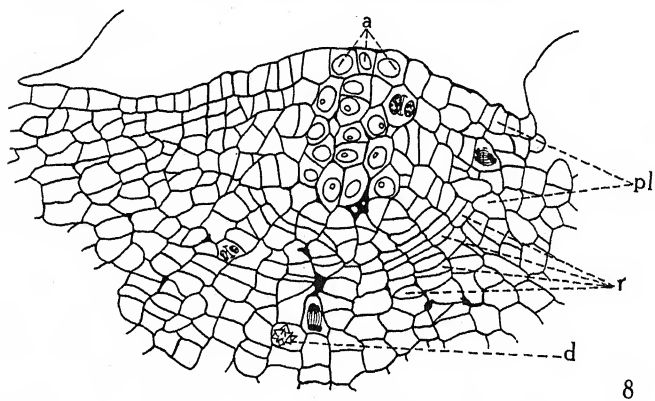
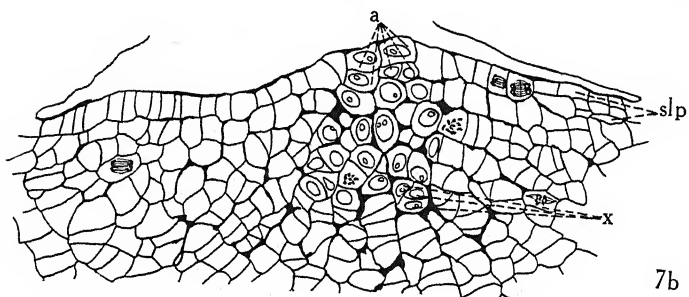
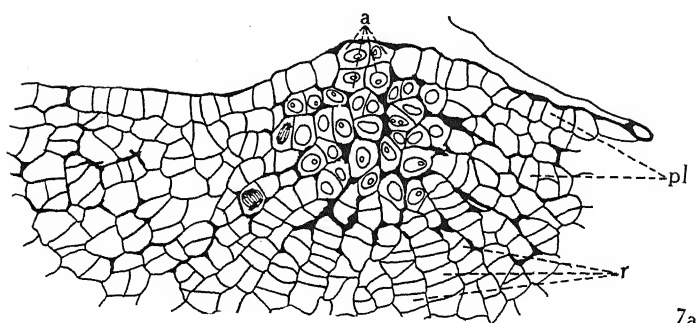
A very puzzling but constant feature of the central mother cells is the irregular and often massive "thickenings" which appear at the corners or along the sides of many of the cells (figs. 5-12; Plates 25-27). Although a detailed physical-chemical investigation has not been made, these "thickenings" seem to represent localized deposits of intercellular substance together with unusually thickened areas in the primary wall.<sup>4</sup> As is shown in figs. 6d, 7a, 7b, 11, and 12, these depositions frequently resemble very strikingly the "corner thickenings" typical of many collenchyma cells. Occasionally, in longitudinal sections, a surface view is obtained of the entire lateral wall of a central mother cell. From this aspect, the wall thickening appears as an irregular reticulum the meshes of which closely resemble simple pits (Plate 25, fig. 2). It is significant that thickened areas, apparently identical to those in the central mother cells, occur sporadically in other zones of the shoot apex, and serve to delimit cell groups of common origin. This is very obvious at the points of origin of the rib meristem from the base of the transition zone (figs. 6a, 6c, 6d, 7a, 7b, 12; Plates 25, 27).

<sup>4</sup> The terms "intercellular substance" and "primary wall" are used in the sense recently defined by Kerr and Bailey (1934).

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Figs. 6a-6d. Successive longisections, at intervals of 14 microns, through the apex of a spur shoot, illustrating the prominence and clear demarcation of the zone of central mother cells and the origin, mode of growth and planes of division of the cells of the peripheral layers and the rib meristem in various regions of the apex. Fig. 6c is approximately median. Note especially the periclinal divisions which have occurred at various points in the surface layer and the characteristically irregular arrangement of the central mother cells. T divisions, associated with the origin of the rib meristem, are shown in the cell groups labeled X in figs. 6c and 6d.





The gradual disappearance of the "thickenings" in the distal regions of the shoot apex suggests that they may experience "reversible" changes during tissue differentiation.

THE PERIPHERAL LAYERS (*Zone IV, fig. 3*)

The expression "peripheral layers" designates a well-defined zone composed of several layers of small, densely cytoplasmic cells. A comparison of transverse and median longisections demonstrates that this zone occupies the flanks of the shoot apex and hence completely surrounds the central mother cells (Plate 26, figs. 1, 2). It should be evident, therefore, that in longisections which pass through the sides, rather than the center of the growing point, a definitely stratified arrangement of cells would be seen. Fankhauser's (1884, taf. II, figs. 7-8) failure to observe the zone of central mother cells and his depiction of "periblem" layers would thus appear to depend upon a study of sections cut in this plane. A similar criticism of the statements of Strasburger (1872) in regard to "histogens" in *Ginkgo* seems justifiable.

From a cytological standpoint, all the cells of the peripheral layers are similar in appearance and, in respect to their small size, deeply stained protoplasts and frequent divisions, correspond to typical primordial meristem. This marked uniformity in structure is interesting in view of the difference in point of origin of the various layers. The outermost or truly surface layer, as I have shown, arises from the apical initial group but by sporadic periclinal divisions undoubtedly augments the subsurface layer (figs. 6c, 6d, 7b, 10; Plate 25, fig. 2). In contrast, the inner cell layers have a separate and independent origin. As is shown in Plates 25 and 27, these layers are continually augmented by the division of the cells at the upper periphery of the zone of central mother cells. In terms of cell activity, this peripheral region truly represents a transition zone between an area of cell enlargement (i.e. the zone of central mother cells) and a region characterized by pronounced meristematic features. From this point of view,

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Figs. 7a-7b. Longisections through the apex of a spur shoot; Fig. 7a approximately median, Fig. 7b 35 microns distal to Fig. 7a. Both figures illustrate the origin of new central mother cells from the inner derivatives of the apical initial group. Note in Fig. 7a the clear demarcation of the U-shaped "transition zone" and in Fig. 7b, a typical T division at X.

Fig. 8. Median longisection through the apex of a spur shoot. Note the anticlinal telophase in one of the central mother cells and the clear definition of the U-shaped transition zone.

Fig. 9. Median longisection through the apex of a spur shoot, illustrating, at the right, anticlinal divisions in several cells of the peripheral layers. Note the polar view of chromosomes in one of the central mother cells.



the central mother cells in *Ginkgo* resemble the situation in the apical meristem of many cryptogams where a zone of large initials merges abruptly into a zone of smaller, dividing cells (cf. Schüepp 1926 p. 6-7). Although it is evident that the sequences of division are variable in the transition zone, transverse sections show that the most recently formed cells are arranged in short radial rows which collectively simulate a cambium (Plate 26, figs. 1, 2). This definitely indicates that the new walls tend to be anticlinal or anticlinal-oblique with reference to the flanks of the shoot apex (figs. 5, 6b, 7a, 8, 11, 12, Plates 25, 27).

Although surface growth is dominant in the zone of peripheral layers (cf. figs. 3, 8, 9) many irregularities in the cell net are produced by periclinal or oblique divisions. Consequently, the peripheral layers show none of the regularity of growth and independence characteristic of the tunica region of the shoot tip in angiosperms (Schmidt 1924). Their closest resemblance is clearly with the outer meristematic layers found in the shoot apices of conifers (Koch 1891, Korody 1937) and certain species of *Lycopodium* (Härtel 1938). Furthermore, as in the forms just named, the regularity of the peripheral layers is noticeably disturbed by the initiation of bud scales and foliage leaves. The inception of these organs is always associated with a local increase in the frequency of periclinal divisions (figs. 5, 10). Frequently, although not invariably, foliar initiation involves the periclinal divisions of the surface layer itself (fig. 5).

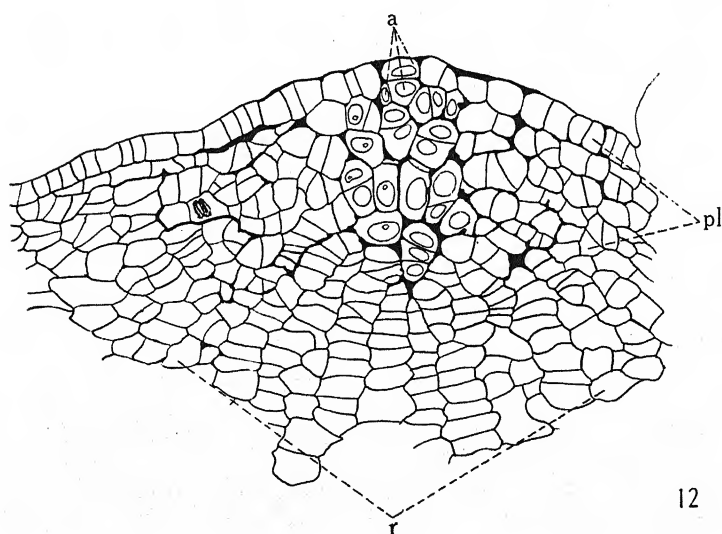
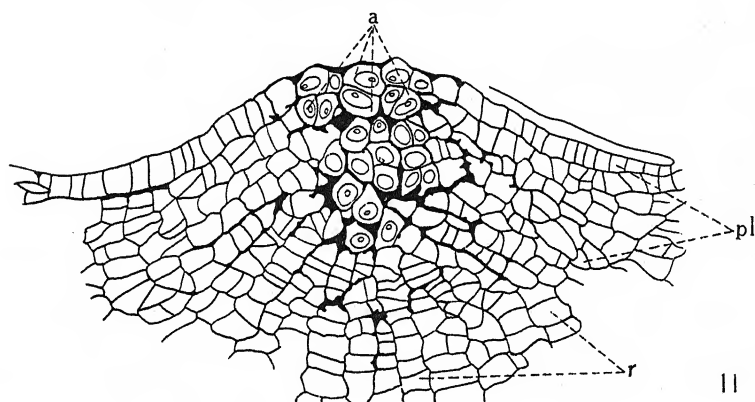
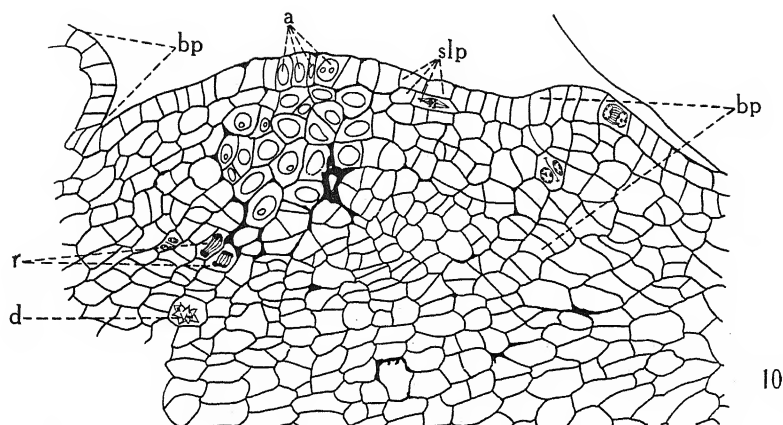
In terms of differentiation, the outer surface layer produces the epidermal system of the shoot while the cortex arises from the inner peripheral layers. Vascular differentiation has not been followed in this investigation but there is evidence that the meristem ring (Barthelmess 1935 p. 214 fig. 5) and hence ultimately the procambium, originates from the innermost layer or layers of Zone IV (cf. fig. 5).

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Fig. 10. Median longisection through the apex of a spur shoot, illustrating at the right the origin of a bud scale primordium from the zone of peripheral layers. The presence of a druse in a cell of the rib meristem at the left is indicative of the abrupt differentiation of the broad pith characteristic of spur shoots.

Fig. 11. Median longisection through the apex of a spur shoot, showing an exceptionally prominent trio of apical initials, from which by anticlinal and periclinal divisions, new surface and internal segments have arisen.

Fig. 12. Median longisection through the apex of a spur shoot, showing clearly the irregular size, shape and mode of segmentation typical of the central mother cells. Note the well defined position of the transition zone in this preparation and the clear rib meristem.



THE RIB MERISTEM (*Zone V, fig. 3*)

The term "rib meristem" has been devised by Schüepp (1926 pp. 18-19) to designate a type of primary meristem which is responsible for the *growth in length* of young internodes, roots, and the petioles of leaves. Growth in a longitudinal direction prevails in the rib meristem and this tissue consists of vertical series of genetically-related cells which have been formed by repeated transverse (i.e. anticlinal) divisions. Although the entire pith region of a shoot axis is produced by rib meristem, interesting differences exist in regard to the point of origin of this meristem in seed plants. In the dicotyledons, the rib meristem forming the pith originates some distance from the surface of the growing point by the active division of the cells of the corpus (Foster 1935, Cross 1936, 1937). In many conifers however, the pith of the shoot axis differentiates far in advance of the other primary tissues and the rib meristem appears as a central core of vacuolating cells which arises *directly* from the inner embryonic layers of the growing point<sup>5</sup> (Koch 1891, Korody 1937). Obviously in both types, the origin of the rib meristem is associated with a more or less abrupt transition from highly meristematic to vacuolating and "stretching" tissue. In *Ginkgo* just the reverse condition occurs since here the transition to rib meristem first involves the *renewal* of mitotic activity in the lower central mother cells. As is true of the origin of the inner peripheral layers, this renewed mitotic activity is accompanied by a decrease in cell size and a greater retention of the nuclear stain (Plates 25, 27).

<sup>5</sup> This fact has been confirmed by the writer in a brief unpublished study of the shoot apex of *Abies venusta*. (Dougl.) K. Koch.

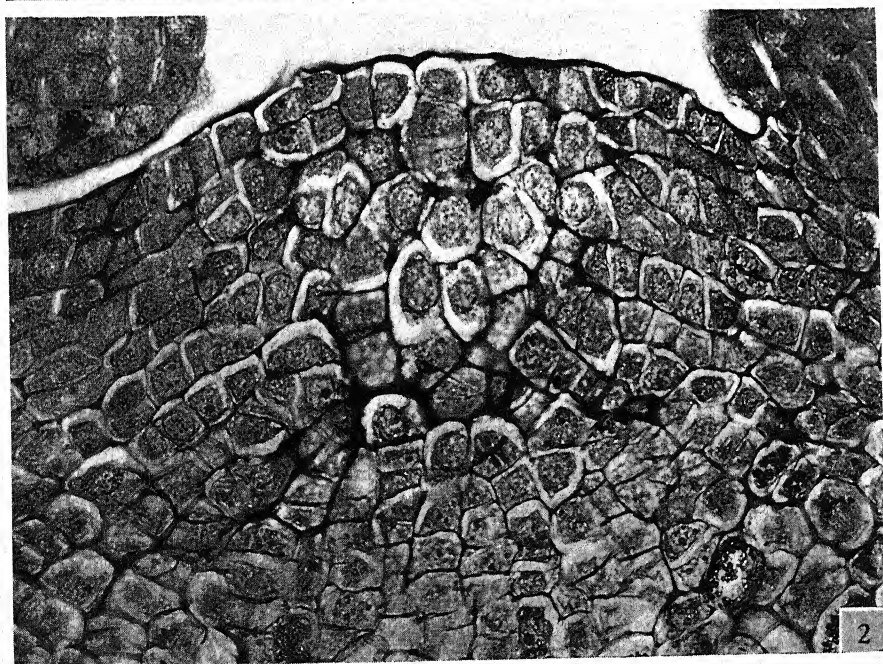
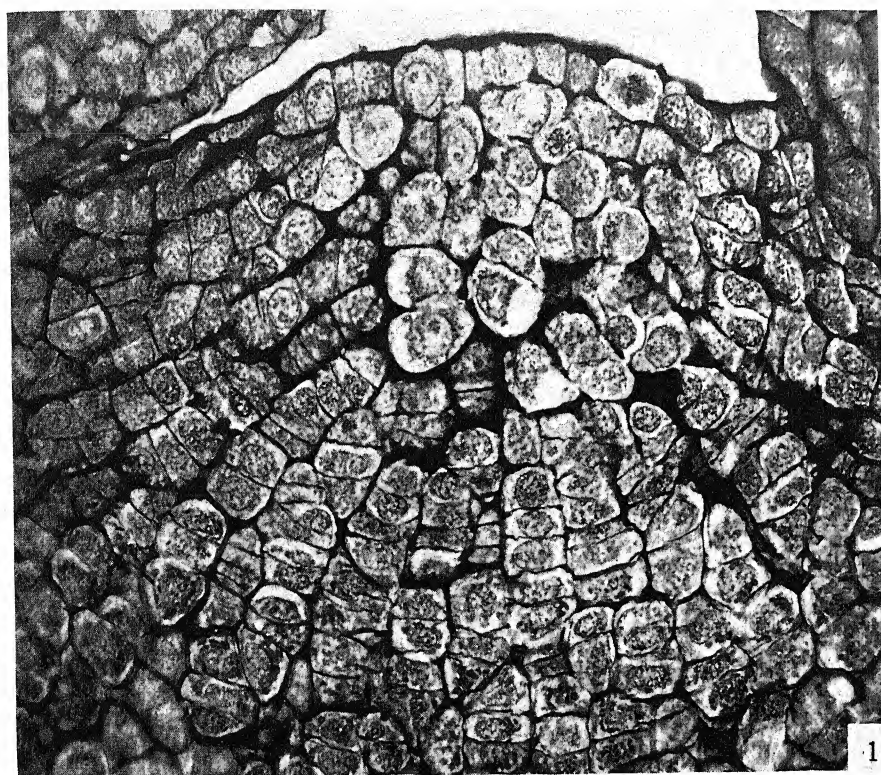
## Explanation of plates

(all figures  $\times 435$ )

## PLATE 25

Fig. 1. Median longisection illustrating the zonal structure typical of the apex of a spur shoot (April 15). The zone of central mother cells, seen in the upper center directly beneath the apical initials, is sharply demarcated from the peripheral layers and the basal zone of rib meristem by the large size, irregular arrangement and lighter-stained appearance of its cells. Note the prominent "wall-thickenings" (stained black) both in the zone of central mother cells as well as in the surrounding zones. An anticlinal metaphase is evident in a cell of the surface layer at the right. The short vertical extent of the rib meristem in this shoot is shown at lower magnification in Text Fig. 1.

Fig. 2. A similar longisection of a spur shoot (April 29). Note especially that the surface layer, on both flanks of the apex, has divided periclinally. To the left and slightly above the prominent metaphase in a cell of the rib meristem, will be seen in surface view the "reticulate" or "pitted" character of the lateral wall of a central mother cell. Note, as in Fig. 1, the rapid maturation of the pith from the short zone of rib meristem.



FOSTER: GINKGO



As seen in median longisection, the transition zone giving rise to the young rib meristem appears as a concave area of small, tabular frequently-dividing cells (cf. especially figs. 5, 6b, 7a, 8, 10, 11, 12 and Plates 25 and 27). The well demarcated appearance of this formative region is the result of the early prevalence of periclinal or periclinal-oblique divisions. Frequently, the repeated formation of periclinal walls in several adjacent cells produces regular short filaments of genetically-related cells (figs. 5, 7a, 10). Often however, following the first periclinal or oblique division, the lower daughter cell divides antclinally thus giving rise to a double series of cells. Such T divisions are illustrated in Figs. 6c, 6d, and 7b by the label X. As noted previously, the wall thickenings of the central mother cells may be "carried over" into the zone of rib meristem and thus aid in the identification of cell groups of common lineage (figs. 6a-6d, 7a-7b, 10, 11, 12; Plates 25, 27).

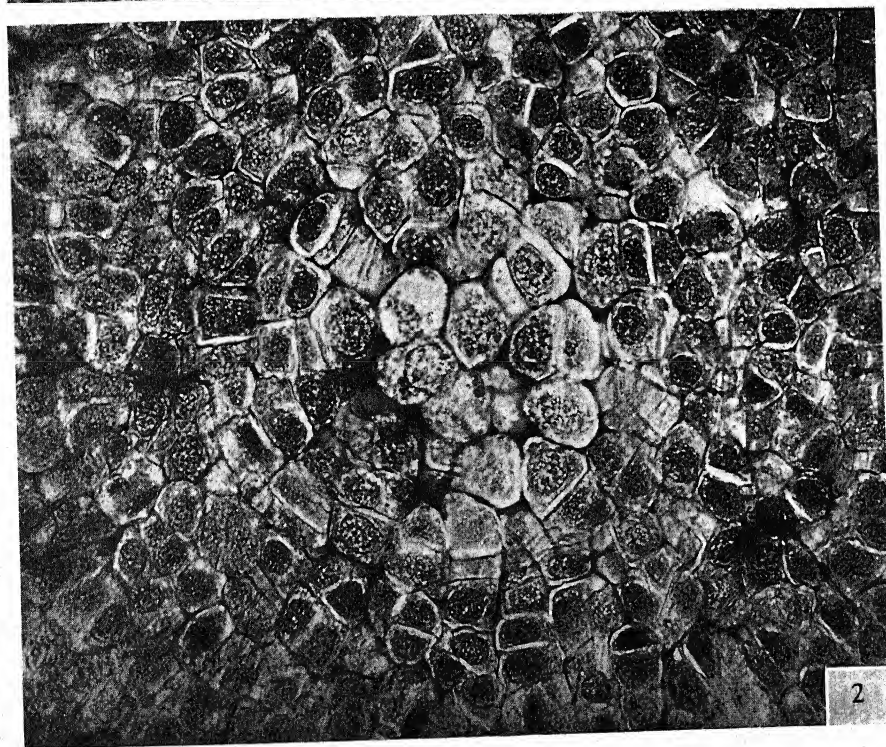
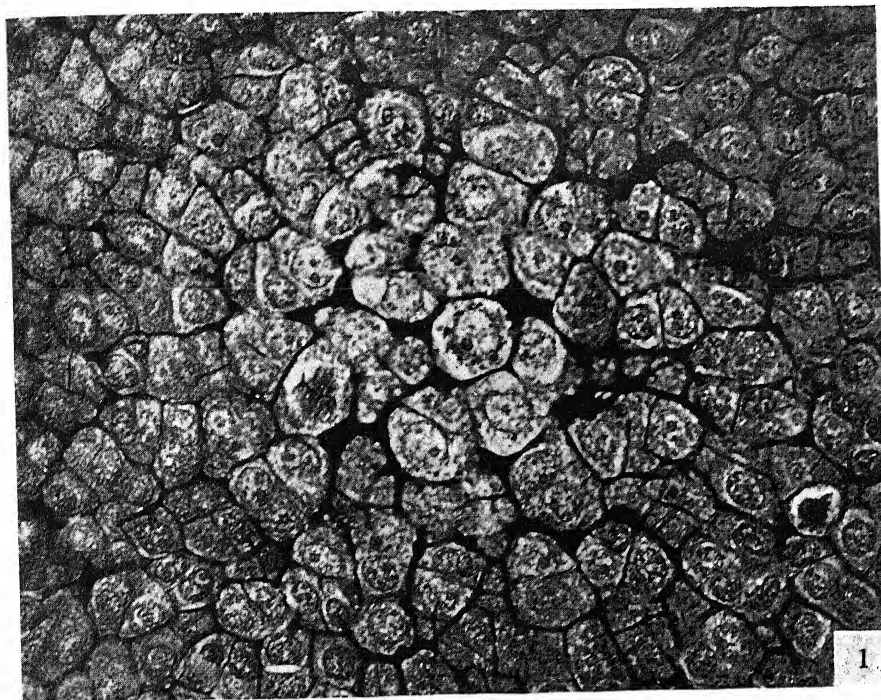
Although the prevailing direction of growth in the young rib meristem is periclinal in respect to the surface of the shoot axis, irregularities in the cell pattern are common and result from periclinal or oblique division of cells at various points. In this way, new chains of cells are formed which appear to "insert" themselves (possibly by "gliding growth") between their neighbors (figs. 6b, 6c, 6d, 7a, 12; Plate 25, fig. 1; Plate 27, fig. 2). A marked difference, which has already been noted, occurs in respect to the duration and mode of growth of the rib meristem in long and spur shoots. In the latter, the rib meristem loses its embryonic character a short distance from the zone of central mother cells and abruptly differentiates into the broad, radially-expanding pith region (fig. 1). Associated with this early cessation of growth, druses frequently appear in many of the cells of the maturing rib meristem (figs. 5, 8, 10). In long shoots however, the rib meristem retains its capacity for growth and cell division for a much longer period of time, and together with the equally active rib meristem beneath the epidermis, makes possible the formation of elongated internodes (fig. 2;

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#### Explanation of Plate 26

Fig. 1. Transverse section of the apex of a spur shoot (April 15) 63 microns below the apical initial group, showing that the large central mother cells (note metaphase) are completely surrounded by the smaller more densely-stained cells of the peripheral layers. The cells of the transition zone, at the margin of the central mother cells, are arranged in irregular radial rows. Compare with Plate 25, figs. 1 and 2.

Fig. 2. Transverse section of the apex of a spur shoot (May 11), 63 microns below the apical initial group depicted in text figure 4. The prominent lightly-stained central mother cells are surrounded by a "cambial-like" transition zone showing a marked radial alignment of cells. Note the anticlinal telophase in one of the cells at the right, and the mitosis in a cell of the peripheral layer at the lower left.



FOSTER: GINKGO



Plate 27, figs. 1, 2). Indeed the unusually active rib meristem in the long shoots of *Ginkgo* would provide excellent material for a study of the rhythmical aspects of mitosis along the lines suggested by the recent investigations of Wagner (1930, 1937).

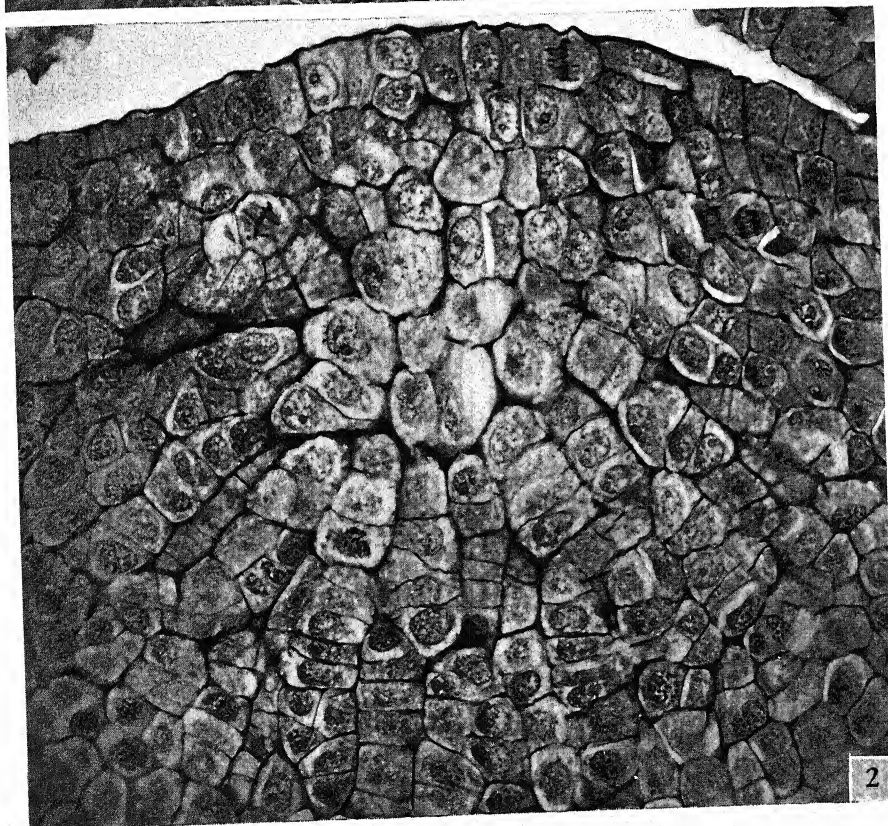
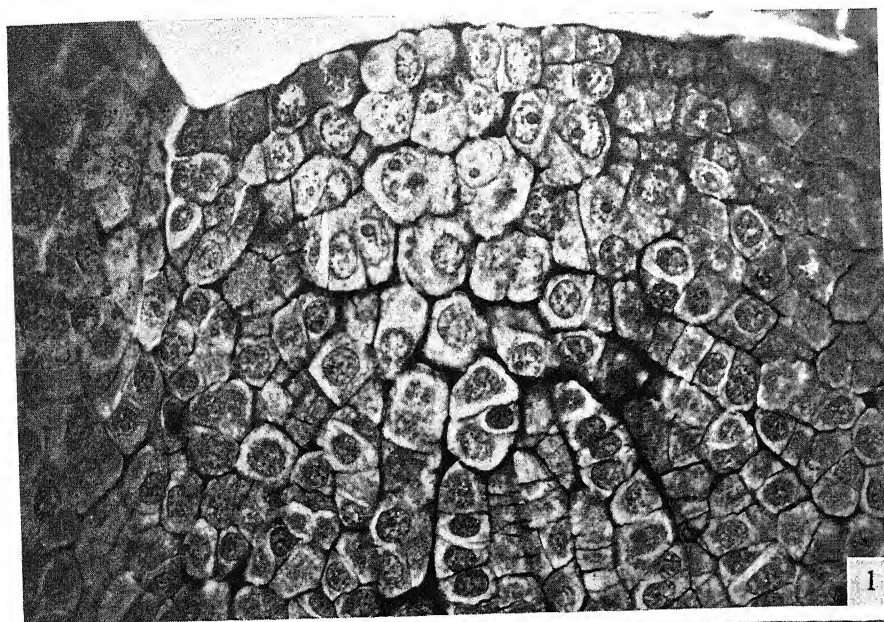
#### DISCUSSION

From a comparative anatomical standpoint, the shoot apex of *Ginkgo* exhibits a type of structure which, in the light of present knowledge, appears unique among vascular plants. On the one hand, it diverges from such vascular cryptogams as *Equisetum* (Vidal 1912) and the leptosporangiate ferns (Bower 1889) in the absence of a definite apical cell and the highly variable sequence of cleavages throughout the meristem. The peculiar cytological features of the apical initials and the central mother cells in *Ginkgo* are, it is true, suggestive of the condition described by Hof (1898) for the apical region of the root of *Pteris*, and for the shoot tip of *Osmunda* (Zirkle 1932, pp. 32-36) but the resemblances are clearly "physiological" rather than "morphological." Furthermore, although such plants as *Lycopodium* (Schüpp 1926 pp. 48-49, Härtel 1938) and the Marrattiaceous genera *Danaea* and *Kaulfussia* (West 1917) agree with *Ginkgo* in the possession of a single tier of apical initials, they differ markedly in the zonal arrangement of their meristems. On the other hand, *Ginkgo* shows but few points of histological similarity with the shoot apices of other gymnosperms. Possibly the closest comparison can be drawn with the Abietaceae which resemble *Ginkgo* in the form and behavior of the apical initials and especially in the absence of a typical "dermatogen" (Koch 1891, Korody

#### Explanation of Plate 27

Fig. 1. Longisection showing the details of structure of the apex of the long shoot illustrated in text figure 2. Note the marked contrast between the large, lightly-stained central mother cells (upper center of figure) and the smaller cells of the peripheral layers and the rib meristem. At the right of the apical initial group will be seen a quartet of cells produced by the "decussate" division of a surface segment. As in the apices of spur shoots (Plates 25 and 26) irregular "wall thickenings" are evident in the zone of central mother cells and help to define genetically-related cell groups in the rib meristem.

Fig. 2. Longisection illustrating the characteristic structure, mode of growth and planes of cell division in the various zones of the apex of a long shoot (April 22). Note the recent periclinal division in a cell of the apical initial group and the anticlinal metaphase in a surface segment at the right. The periclinal division of the surface layer is evident on each flank of the apex. Mitoses are also shown in a central mother cell (upper left) and in cells of the peripheral layers (upper right). Note especially the active propagation of the filamentous groups of rib meristem from the basal margins of the zone of central mother cells.



FOSTER· GINKGO

1937). However, the well-defined zone of central mother cells is peculiar to *Ginkgo* and, as far as I am aware, is not duplicated in the shoot tips of the conifers. In the latter, according to the classical investigations of Koch (1891), the meristem is arranged in two zones which are clearly defined as to cell structure and mode of growth, viz.: (1) an outer "Hüllgewebe" composed of several layers of typical meristematic cells which produce the epidermis, cortex, procambium and foliar organs and (2) an inner core or "central tissue" of somewhat vacuolated cells which form the pith. It is clear from Koch's descriptions and excellent drawings that unlike the condition in *Ginkgo*, the rib meristem (i.e. his "central tissue") in the shoot apices of conifers is propagated directly from a small subterminal group of "mother cells." The latter, except in their position and predominant periclinal division, resemble in size, form and dense cytoplasm the neighboring cells of the "Hüllgewebe" and hence show none of the definitive characteristics of the central mother cells of *Ginkgo* (cf. Plates 25-27). Koch's observations have been confirmed in a recent study by Korody (1937) for the shoot tips of *Abies*, *Picea* and *Pinus*. This investigator makes a sharp distinction between the "Bildungselement" (i.e. the "corpul-like" terminal region of the apex) and the "Strukturelemente" (i.e. the embryonic layers and the central tissue) in the growing point. Her descriptions, drawings and photomicrographs again emphasize that the "mother cells," from which the two "structural elements" are propagated, are not comparable either in extent or histological features to the central mother cells of *Ginkgo*. On comparative grounds it is interesting to note that Härtel (1938 pp. 165-166) finds a marked resemblance between the general structure and growth of the shoot apex in the conifers and that typical of various species of *Lycopodium*. In the latter however, only the subapical "mother cells" are polygonal in form and the "central tissue" arising from them consists of small elongated spindle-shaped cells which differentiate into the vascular tissue of the protostele.

In view of the archaic and probably primitive morphology of *Ginkgo*, it would be tempting to argue that the distinctive structural features of its shoot apex typify a "primitive stage" in the evolution of the apical meristem of seed plants. For the present however, a rather conservative viewpoint seems preferable because of the debatable relationship between *Ginkgo*, the conifers and the flowering plants (cf. Sprecher 1907 p. 198) and Chamberlain (1935 p. 433-436) and particularly because our knowledge of the comparative anatomy of apical meristems in the spermatophytes is still very meagre. Strasburger (1872) and Schüepp (1926 pp. 50 and 55) have both suggested that the architecture of the shoot apex in gymnosperms serves to articulate the condition found in *Lycopodium* with

that typical of angiosperms. Indeed in *Araucaria* according to Strasburger (1872, taf. XXIII, fig. 13) the outer surface layers of the shoot correspond in mode of arrangement to Hanstein's (1868) "dermatogen" and "periblem" and hence resemble the tunica zone of a dicotyledon. Nevertheless our present knowledge seems insufficient to deduce with confidence the phylogenetic development of the stratified condition of the apical meristem typical of the angiosperms. Korody (1937) has approached the problem from the theoretical standpoint advanced by Buder (1928). She maintains that because of the single tier of apical initials in *Abies*, *Picea* and *Pinus*, the entire apical meristem may be homologized with the corpus region of the shoot apex in angiosperms. A similar conclusion is reached for *Lycopodium* by Härtel (1938). I cannot agree with this interesting theory however, because it is based upon too rigid a morphological distinction. In my opinion, tunica and corpus represent *interdependent growth zones* in an apical meristem and as such, one cannot exist independently of the other. Consequently, in agreement with Schüepp (1926, 1927) I would regard the condition in the Abietaceae as indicative of a transitional stage in the evolution of the zonation typical of the shoot tip in angiosperms. From this viewpoint, it may subsequently prove correct to interpret the structural pattern in *Ginkgo* as an even lower stage in the evolutionary sequence.

In conclusion, it seems fitting to emphasize the need for a complete re-examination, along broad comparative lines, of the architecture and modes of growth of the shoot apex in gymnosperms. It would be particularly interesting to explore the situation in the cycads, since they play such an important rôle in evolutionary theory. The older literature dealing with the apical meristem in gymnosperms seems to have dealt largely with the question of the existence of an apical cell (for resumé of the literature cf. Koch 1891, Schüepp 1926 and Korody 1937). However, the recent studies of Helm (1932), Louis (1935), Barthelmess (1935) and Kaplan (1937) indicate the increasing tendency to emphasize the behavior of *entire cell complexes* during embryonic growth and differentiation, rather than the "destiny" of individual cells. This attitude has guided the present investigation and if consistently applied in comparative studies should increase our understanding of the fundamental interrelationship between growth and structure in the shoot apex of vascular plants.

#### SUMMARY

The meristem of the apex of spur and long shoots in *Ginkgo* is not uniform in structure but is segregated into five distinctive zones characterized by the size, staining reactions and mode of growth of the component cells.



The uppermost zone is represented by the apical initial group, from which by anticlinal and periclinal divisions respectively, the surface layer and the internal cells of the shoot apex originate. There is no regular sequence in the successive planes of division of the cells of the apical initial group, and the cell net is correspondingly variable in pattern. Furthermore, periclinal divisions are not restricted to the apical initials but occur at any point in the surface layer.

Directly beneath the apical initial group is found the zone of central mother cells which constitutes the most unique feature of the shoot apex. In their large size, irregular arrangement, relatively infrequent divisions and lightly stained protoplasts, the central mother cells diverge from the structural features usually associated with the primordial meristem of seed plants. It is concluded that volume growth predominates in this zone which, in this respect, is analogous to the corpus region of the angiospermous growing point. A puzzling feature of the central mother cells is the presence of thickened areas at the corners or along the sides of many cells or cell groups. These thickenings are provisionally interpreted as local and temporary depositions of intercellular and primary wall substance.

The lateral and basal margins of the central mother cells represent a "transition zone" from which, by means of renewed mitotic activity, are propagated respectively the bulk of the zone of peripheral layers and the zone of rib meristem.

The zone of peripheral layers, because of the small, deeply stained frequently dividing cells which compose it and the notable emphasis on surface growth might be compared with the tunica region of the growing point in angiosperms. However, periclinal divisions may occur at any point so that there is no constancy in the number of cell layers. In terms of differentiation, the epidermis, cortex and procambium of the shoot axis arise respectively from the outer, middle and innermost of the peripheral layers.

The zone of rib meristem consists of short chains of cells in which growth in length and transverse divisions predominate. The number of filamentous series is continually augmented by periclinal or oblique divisions. In the spur shoot, the closely crowded internodes result from the limited period of activity of the rib meristem which, a short distance from the growing point, gives rise to the broad rapidly maturing pith. By contrast, internodal extension in the long shoot is related to the much greater capacity for continued growth and cell division in the rib meristem of both pith and cortical regions.

The shoot apex of *Ginkgo* possesses a unique type of structure which is not duplicated in vascular cryptogams or seed plants. It is suggested that in some respects however it may typify a "primitive stage" in the evolu-

tionary development of the tunica-corpus regions typical of the shoot apex in angiosperms.

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## Some New and Interesting Late Tertiary Plants from Sucker Creek, Idaho-Oregon Boundary\*

HELEN V. SMITH

(WITH PLATES 28 AND 29)

In this paper are descriptions of six new species and records of seven species not previously reported from Sucker (i.e., Succor) Creek. Sucker Creek is mostly in Malheur County, southeastern Oregon, and flows in a northerly direction near the Idaho-Oregon boundary line finally crossing into Owyhee County, Idaho, where it empties in the Snake River.

Collections were made from the Miocene lake beds during the summers of 1931, 1932, 1934, and 1936 from three principal localities. In the lower part of the valley specimens were obtained from several beds close to the old Ballantyne Ranch house in Idaho and two or three miles farther up the creek near an old coal prospect. In the upper part of the valley the collections were made from several beds within three or four miles of the Rockville, Oregon, postoffice. There do not appear to be any notable variations among the fossils of the same species collected at the various localities, and the plant associations represented are apparently the same and of the same age. However, the specific localities for the new species are reported here since more extensive studies may eventually indicate locality variation in the flora.

### DESCRIPTION OF SPECIES

#### *Polypodiaceae*

*Woodwardia deflexipinna* n. sp. (Plate 28, figs. 3, 6). Outline of frond unknown; pinnae lanceolate; sterile and fertile pinnae alike; pinnae cut three fourths of the distance to the midrib; pinnules broadly lanceolate, rounded at the apex, broadest at base, 1 cm. long, not auricled; margin entire and slightly revolute in some specimens; mid-vein of pinnae and pinnules with a single series of oblong, very slightly oblique areoles on each side; outer veins free, ending along the margin; sori linear or oblong, one to each areole.—Type, no. 20014, Mus. Paleont., Univ. of Mich. Collected near Rockville, along the Strode Ranch road east of the postoffice.

The living species to which this fossil seems to be most closely allied is *Woodwardia virginica* (L.) Smith (Plate 28, fig. 2), the common chain fern of eastern North America. In venation, size and distribution of the sori, the entire margin, and rather spreading pinnae the two forms are practically identical.

Among the eight fossil species of *Woodwardia* from the western states this is closest to *W. Maxoni* Knowlt. and *W. crenata* Knowlt. from the

\* Papers from the Department of Botany of the University of Michigan no. 661.

Eocene. The Sucker Creek species differs from these particularly by having an entire instead of serrate margin and in the smaller size of the pinnules.

At one locality on the east side of the valley near Rockville, Oregon, this species is extremely abundant. A ledge several inches thick is a mass of fern fragments and many immature rolled up fronds are also common.

#### *Equisetaceae*

*Equisetum octangulatum* n. sp. (Plate 28, fig. 1). Stem 4.5 mm. wide; internode 3.3 cm. long; 4 or 5 longitudinal ribs visible; 5 small branch scars, and no leaves visible at the node.—Type, no. 20013 Mus. Paleont., Univ. of Mich. Collected near the Ballantyne Ranch.

The fragment figured here is the only well preserved specimen in the collection. In spite of its poor representation it seems to be advisable to report the species.

#### *Pinaceae*

*Pinus* sp. (Plate 28, fig. 8). Needles short, in groups of three; rigid; slender, sharply pointed; 2.7 cm. long.

These needles differ from those assigned to *P. Knowltoni* Chaney (3) in being more rigid, narrower, and considerably shorter. They are very straight and not curved as they often are in *P. Knowltoni*.

The short *Pinus* needles from Salmon, Idaho, figured by Brown (1) in Plate 45, fig. 10 may represent the same species.

#### *Betulaceae*

*Betula Bendirei* Knowlt. (Plate 29, fig. 3). The single specimen referred to this species is practically identical with leaves of the living *B. occidenta-*

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#### Explanation of Plate 28

Fig. 1. *Equisetum octangulatum* H. V. Smith. Type; Mus. Paleont., Univ. of Mich. no. 20013.

Fig. 2. *Woodwardia virginica* (L.) Smith. Specimen from Bloomfield, Michigan in the Herbarium, Univ. of Mich.

Fig. 3. *Woodwardia deflexipinna* H. V. Smith, Type; Mus. Paleont., Univ. of Mich. no. 20014.

Fig. 4. *Acer Buergerianum* Miq. Specimen from the Botanical Gardens, Univ. of Mich.

Fig. 5. *Acer Bolanderi* Lesq.

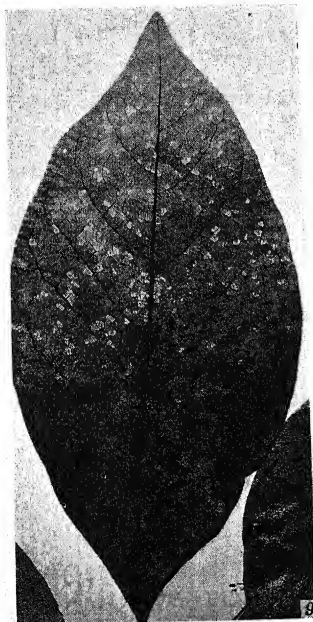
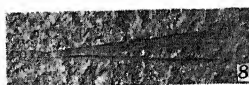
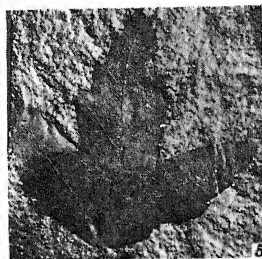
Fig. 6. *Woodwardia deflexipinna* H. V. Smith. Fertile pinnule.

Fig. 7. *Dipteronia insignis* (Lesq.) R. W. Brown.

Fig. 8. *Pinus* sp.

Fig. 9. *Nyssa aquatica* L. Specimen from Richland Co., Ohio in Herbarium, Univ. of Mich.

Fig. 10. *Nyssa oregonensis* H. V. Smith. Type; Mus. Paleont., Univ. of Mich. no. 20015.



HELEN SMITH: TERTIARY PLANTS

*lis* Hook. This living species occurs along the borders of streams, and margins of meadows in rich moist humous, sandy, and rocky soils. It is found from southwestern British Columbia to northern Washington and east to the Rocky Mountains.

Among fossil species this seems to be most similar to *B. lacustris* MacG. from Trout Creek, Oregon. The Trout Creek species is closely related to *B. fontinalis* Sarg. which was long confused with *B. occidentalis*.

Although the specimen in this collection does not correspond exactly with that figured by Knowlton (4), it is referred to his species because of its resemblance to *B. occidentalis* which he considered to be similar to his fossil. It also answers to Knowlton's description.

#### *Fagaceae*

*Quercus malheurensis* n. sp. (Plate 29, fig. 1). Leaves subcoriaceous, rather small, length up to 7 cm. (estimated), width to 4.5 or 5 cm.; sparsely lobed; lobes rounded, not bristle tipped, one or two on each side of leaf, the lower much larger than the upper; apex of leaf broadly rounded; base cuneate; midrib and lateral veins strong, somewhat undulate; principal lateral veins extending to the tips of the lobes; smaller veins opposite or alternate, relatively weak, curving upward in an irregular manner and becoming effaced; tertiary venation not visible; ultimate venation a fine regular reticulum.—Type, no. 20010 Mus. Paleont., Univ. of Mich. Collected near the old Ballantyne Ranch house.

These leaves belong to the white oak group and resemble some of the sparsely lobed small leaves of *Q. alba* L. They differ from previously figured fossil oaks of this group chiefly in the small number of lobes and small size, and when a larger series of specimens becomes available may be found to represent a small form of some previously described species. For the present, however, it would be merely guessing to place this fossil with any described form, and there would be the great disadvantage that it might lead to confusion in the record of the other species to which it was referred.

#### *Rutaceae*

*Ptelea enervosa* n. sp. (Plate 29, fig. 6). Samara almost round, winged all around, 2 seeded; seed cavity 4 mm. wide, 6 mm. long; total length of samara 1.7 cm.; total width 1.8 cm.; wing firm, with no visible venation.—Type, no. 20011, Mus. Paleont., Univ. of Mich. Collected near the old Ballantyne Ranch.

A single samara was found in the lower Sucker Creek Valley. It is readily distinguishable from *P. miocenica* Berry by its smaller size and the firm wing with no visible venation. Among living forms examined this is closest to *P. mollis* M. A. Curtis var. *cryptoneura* Bartlett (Plate 29, fig. 7). The living plant has samaras of the same size and shape and the veins are



likewise very indistinct. It occurs in the southeastern states. No leaves referable to *Ptelea* have been observed in the collection.

*Anacardiaceae*

*Rhus oregonensis* n. sp. (Plate 29, fig. 9). Leaf membranaceous, 4.5 cm. wide, 6.5 cm. long; palmately deeply three-lobed or compound; leaflets pinnate; terminal leaflet broadest just below the middle, tapering cuneately below and having two pairs of small rounded lobes or teeth above; apex apparently acuminate; lateral leaflets with three lobes above and four below, the basal inferior lobes of each lateral leaflet much larger, quite distinct and extending downward; secondary veins enter the shallowly toothed lobes; tertiary venation obsolete; sinuses between the three main lobes very narrow.—Type, no. 20012 Mus. Paleont., Univ. of Mich., collected near Rockville, Oregon.

The leaf was compared with specimens of three genera that may have leaves of this general type; *Acer*, *Panax*, and *Rhus*. Superficially similar leaf forms are found in *P. trifolium* L. and *P. quinquefolium* L. The differences are rather marked, neither has the small prominent basal lobe, the former has smaller more numerous marginal teeth and the latter has much narrower lobes than the fossil. As these are both low-growing herbaceous forms the chances of anything related to them entering the fossil record would be extremely slight. Various deeply dissected trifoliate leaves of *Acer*, especially of *A. Negundo* L. and *A. glabrum* Torrey approach this type. The greatest degree of similarity, however, is found with various species of *Rhus*, especially with *R. trilobata* Nutt. and to some extent with *R. Toxicodendron* L. The fossil differs from *R. trilobata* chiefly in having the small basal lobes arising almost or quite at the top of the petiole.

No similar species of *Rhus* have been previously reported from the western Miocene. As pointed out by Brown (2) the leaf described as *R. diluvialis* Arnold from Carter Creek is probably a specimen of *Acer Osmondi* Knowlt.

*Aceraceae*

*Dipteronia insignis* (Lesq.) Brown. (Plate 28, fig. 7). A single specimen that unfortunately has a small portion missing appears to be identical with the samaras figured by Brown (1) as *Dipteronia insignis*. He says that this species is related to *D. sinensis* Oliver of central and western China. No leaves referable to this species have been detected in the Sucker Creek material.

*Acer Bendirei* Lesq. (Plate 29, fig. 4) Under this name Brown (1) includes the leaves and fruits of *Acer* previously designated by several different names, that appear related to *A. macrophyllum* Pursh. Three samaras but no leaves referable to this species, are included in my Sucker Creek collections.



*Acer Bolanderi* Lesq. (Plate 28, fig. 5; Plate 29, fig. 8). This species is represented by several small specimens that are closely similar to the small leaves figured by Lesquereux (6) from the Auriferous Gravels of California. The leaves are trilobate, with entire or sparsely toothed margins, broadly cuneate base and straight or curved midrib.

The leaves were originally compared with *A. tripartum* Nutt. as to shape and with *A. grandidentata* Nutt. as to size and consistency. In writing about the specimens from Eagle Creek Chaney (4) pointed out certain similarities with *A. saccharum* Marsh. However, a closer resemblance is evident with *A. Buergerianum* Miq. (Plate 28, fig. 4). The leaves studied were taken from plants growing at the Botanical Gardens of University of Michigan. The leaves of this species are like the fossils in the small size, prominent primary veins, character of the lobes, and the weak or obscure tertiaries. *A. Buergerianum* is native to Japan and China.

*Acer negundoides* MacG. (Plate 29, fig. 5). This species was described from seeds that resemble those of the living *A. Negundo* L. It was described by Mac Ginitie (7) from Trout Creek and has since been reported from a number of western Miocene localities. The samaras do not usually occur in association with perfect leaflets and few figures of the leaves have been given. LaMotte (5) has recently figured a complete leaflet of an *A. Negundo* type found in association with the fruits. His collection contained a single lateral leaflet that differs in several particulars from the one figured here. The leaflet of *A. Negundo* figured (Plate 29, fig. 2) for comparison was taken from a tree at the Botanical Gardens of the University of Michigan and came from Nebraska. No samaras referable to this species have been noted in this collection.

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#### Explanation of Plate 29

Fig. 1. *Quercus malheurensis* H. V. Smith. Type; Mus. Paleont., Univ. of Mich. no. 20010.

Fig. 2. *Acer Negundo* L. Leaflet from Botanical Gardens, Univ. of Mich.

Fig. 3. *Betula Bendirei* Knowlt.

Fig. 4. *Acer Bendirei* Lesq.

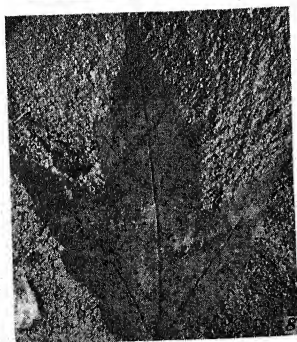
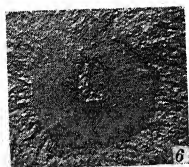
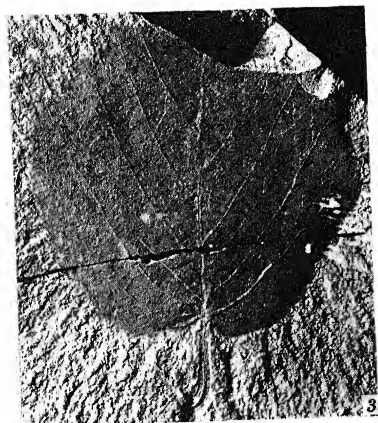
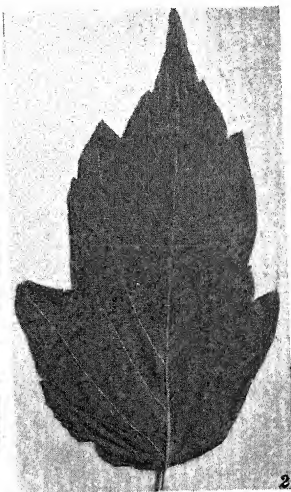
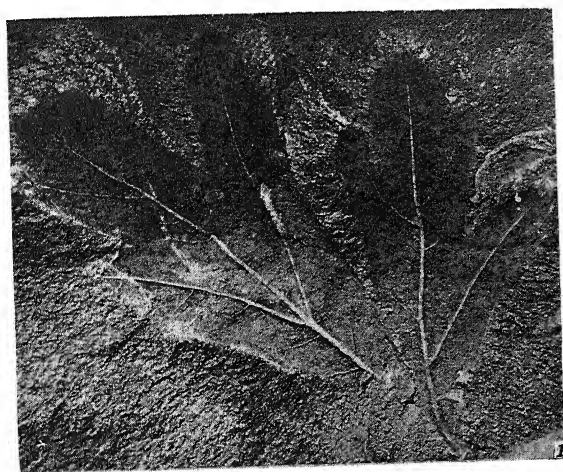
Fig. 5. *Acer negundoides* MacG.

Fig. 6. *Ptelea enervosa* H. V. Smith. Type; Mus. Paleont., Univ. of Mich. no. 20011.

Fig. 7. *Ptelea mollis* M. A. Curtis var. *cryptoneura* Bartlett. Specimen from McDuffie Co., Georgia, in Herbarium, Univ. of Mich.

Fig. 8. *Acer Bolanderi* Lesq.

Fig. 9. *Rhus oregonensis* H. V. Smith. Type; Mus. Paleont., Univ. of Mich. no. 20012.



HELEN SMITH: TERTIARY PLANTS

*Cornaceae*

*Nyssa oregonensis* n. sp. (Plate 28, fig. 2). Leaves subcoriaceous, 9.5 cm. long, 4.3 cm. broad; ovate, widest about the middle, tapering to an acuminate apex and cuneate base; margin entire; midrib fairly strong, straight or slightly curved, secondaries about 10 pairs, parallel, alternate or occasionally subopposite, arising at an acute angle, finer nervation a very fine distinct reticulum.—Type no. 20015 Mus. Paleont., Univ. of Mich. Collected near Rockville, Oregon.

This sub-coriaceous entire-margined leaf is similar to leaves of *Benzoin aestivale* (L.) Nees and *Diospyrus virginica* L., but is still more like certain leaves of *Nyssa aquatica* L. (Plate 28, fig. 8). This single specimen leaves little doubt as to the presence of *Nyssa* of the *N. aquatica* type in the Sucker Creek beds. No fruits of *Nyssa* are included in this collection.

Three leaf species of *Nyssa* have been described from the western Miocene, but all differ in significant ways from this species. *N. crenata* Chaney from Bridge Creek and Eagle Creek has a crenate margin, a greater regularity in the spacing of the secondaries, and has percurrent tertiaries. *N. hesperia* Berry differs markedly from this species in the less regular venation, the arching of the secondaries well within the margin, the percurrent tertiaries and in the much broader shape. *N. Knowltoni* Berry is more elliptical, has a more prominent midrib and distinctly percurrent tertiaries.

The five modern species of *Nyssa* are native to southwestern Asia and southeastern America. *N. aquatica* occurs in cypress and other swamps from Virginia to Missouri and southward to Florida and Texas.

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## New species of cacti from Guatemala, Mexico and Texas\*

ELZADA U. CLOVER  
(WITH 7 FIGURES)

**Echinocereus Gentryi** sp. nov. (figs. 1, 2, 3). Caespitosus, caulibus 2-4, decumbentibus vel erectis, 6-15 cm. altis, 2-2.5 cm. crassis; costis 5, rectis, summitate spiralibus, vix tuberculatis; spinis 8-12 lateralibus radiatis, porrectis, acicularibus, albis vel fuscis; centrali saepe solitaria; omnibus fuscis; basi bulbosis, deciduis; areolis 1 mm. latis, rotundis; floribus magnis, 6-8 cm. longis, 5-6 cm. latis, roseis; segmentis perianthii 5-seriatis, stylo albo; stigmatibus lobis 8, viridibus; filamentis numerosis, antheris rufis; fructibus viridescentibus. Specimen typicum vivum ex loco "Saucito" dicto in Sonora, Mexico conservatum est in Horto Botanico Universitatis Michiganensis; atque floribus siccis in Herb. Mich.

**Echinocereus Gentryi** n. sp. (figs. 1, 2, 3). Caespitose, stems procumbent to ascending, few, jointed 6-15 cm. high, 2-2.5 cm. broad; ribs 5, indistinct, spiral, especially toward the top, tubercles scarcely visible; areoles minute, 1 mm. or less across, circular, 3-4 mm. apart; radial spines 8-12, acicular, 1-2 mm. long, bulbous at the base, more or less deciduous, on very young stems white, often 4-5 mm. long; on new growth of older stems, shorter, brownish; young areoles white woolly, in age naked; central spine usually solitary, rarely 2-5, similar to radials, sometimes darker brown; blossoming in April from areoles 5 to 7 cm. from the tip, flower funnellform, 6-8 cm. long, 5-6 cm. across, tube 3-4 cm. long, perianth segments in 5 whorls, the outer ones bract-like, curling back, olive-drab, inner segments amaranth pink to Tyrian pink, lanceolate, apiculate; style exerted, white to very pale green, stigma lobes 7-8, emerald green; filaments pink above, white below; anthers red; pollen deep yellow; ovary globose, 1.5 cm. across at maturity, greenish, bracts very small, olive-drab, areoles circular, containing somewhat cobwebby wool, spines 8-20, white to pinkish brown, 4-5 mm. long, longer on flower tube than on ovary.

Flowers in the greenhouse open fully about 3:00 p.m. and remain almost fully open all night.

This species is apparently closely related to *E. subinermis* described by Salm-Dyck in 1856 from Chihuahua, Mexico. That species, however, has a shorter flower tube, style included, and is yellow. The author was unable to get either herbarium of living specimens of *E. subinermis*, since it apparently has never been recollected. Comparisons were made from descriptions and photographs. This new species was collected at Saucito, Sonora, Mexico by H. S. Gentry in 1932.

**Echinocereus Steereae** sp. nov. (fig. 4). Simplex vel caespitosus, caulibus erectis, 8-12 cm. altis, ca. 6 cm. crassis; costis 16-18, tuberculis parvis; spinis

\* Papers from the Department of Botany and the Botanical Gardens of the University of Michigan, No. 662.



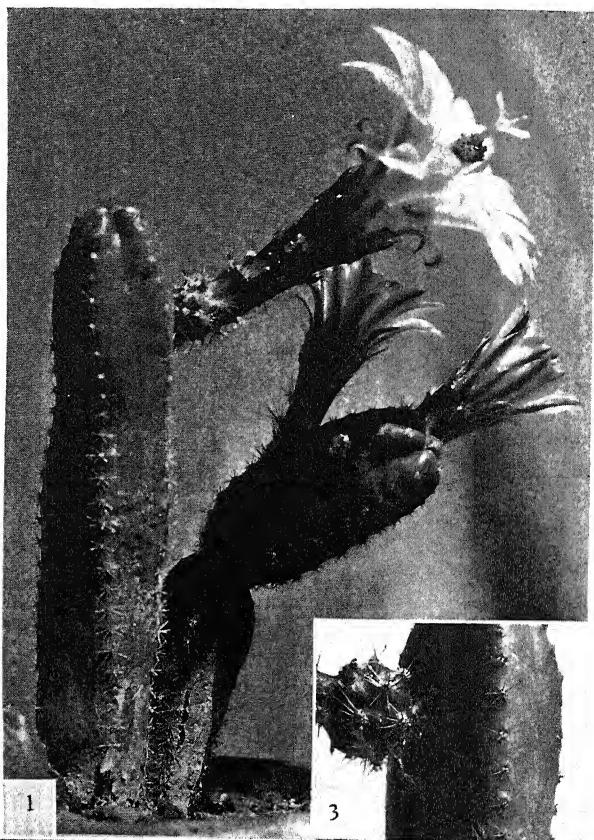


Fig. 1. *Echinocereus Gentryi* in flower. (About two thirds natural size.)

Fig. 2. Flowers of same.

Fig. 3. Fruit of same. (About natural size.)



lateralibus 16-24, acicularibus, albis vel rosaceis, centralibus plerumque 3-5, in serie singula verticali dispositis, areolis ellipticis; floribus magnificis, 10-11 cm. longis, 14-15 cm. latis, segmentis perianthii 5-seriatis, exterioribus, fusco-olivaceis margine, pallide viridibus parte media roseopurpureis; stylo viridi; stigmatis lobis 12; filamentis viridibus; antheris luteis; fructibus ignotis. Specimen typicum vivum ex Montibus Texensibus "Chisos" dictis conservatum est in Horto Botanico Universitatis Michiganensis, Ann Arbor, Michigan; atque floribus siccis in Herb. Mich.

**Echinocereus Steereae** n. sp. (fig. 4). Plant simple or caespitose, with pinkish white appearance, not at all banded, largest stem seen 12 cm. long, 6 cm. across; ribs 16-18, tubercles distinct, small, flattened dorso-ventrally, alternating with those on adjoining ribs; areoles short-elliptic, if young densely white-wooly (wool lacking in older areoles), 5-7 mm. apart; radial spines 16-24, interlocking, 3-5 spines at the upper end of areole shorter, others about equal, spreading and slanting downward at an angle of 45 degrees; central spines 3-5, usually in a single row, bulbous at the base, shorter than the lower radials, stouter than the upper radials, usually a deeper pink. Flowering in April from areoles almost halfway up the stem to within 3 cm. of the top; flowers ascending or standing at right angles to the stem, very showy, 10-11 cm. long, 14-15 cm. across; perianth segments in 5 whorls, the inner three rose-purple with whitish margins, 7-7.5 cm. long, 2 cm. across near center of segment, very narrow at the base and obtuse to cuspidate at the tip, somewhat erose; tinged with greenish-yellow toward the inside center, grading to deep turtle green at the center; outermost segments uneven, 1.5-3 cm. long, tapering to a very narrow tip, olive-drab in midline, pale green and petal-like at the smooth margin, second whorl 5-7 cm. long, olive-drab in midline, pale green tinged with rose-purple toward the margin; style extending 1 cm. beyond the stamens, white, 2 mm. in diameter, included, stigma lobes dark green, 12, somewhat fused, slightly recurved, decurrent; filaments greenish, anthers pale yellow; ovary 5 cm. long, 1.75 cm. across, its areoles 1 cm. apart, circular, prominently white-wooly, with spines 14-15, spreading, rigid, acicular, 4-5 mm. long, white with brown tips; bracts bright green, tipped with pink, 2 mm. long, narrow; fruit unknown.

Collected by Mrs. Lois Steere in the Chisos Mts., western Texas, March, 1937.

**Rhipsalis Bartlettii** sp. nov. (figs. 6, 7). Ramosissima, ramis pendulis, filiformibus, dichotomis, rarius verticillatis, pallide viridibus; areolis prominentis, dense lanatis, lana lutea-fusca; fructibus albis, globosis. Specimen typicum siccum legit H. H. Bartlett sub numero 12720 ex "Uaxactun," Petén, Guatemala, in Herb. Univ. Mich.

**Rhipsalis Bartlettii** n. sp. (figs. 6, 7). Hanging epiphyte, branches 2 m. long, weak and pendent, branching dichotomous, sometimes verticillate, light green, outer joints often less than 1 mm. in diameter, areoles prominent, filled with

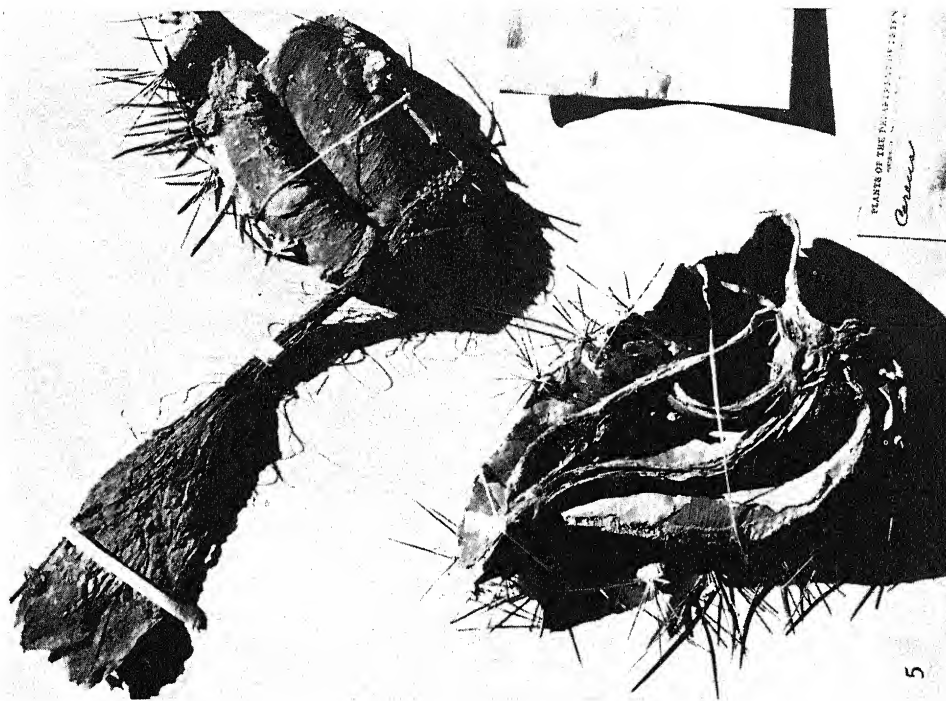
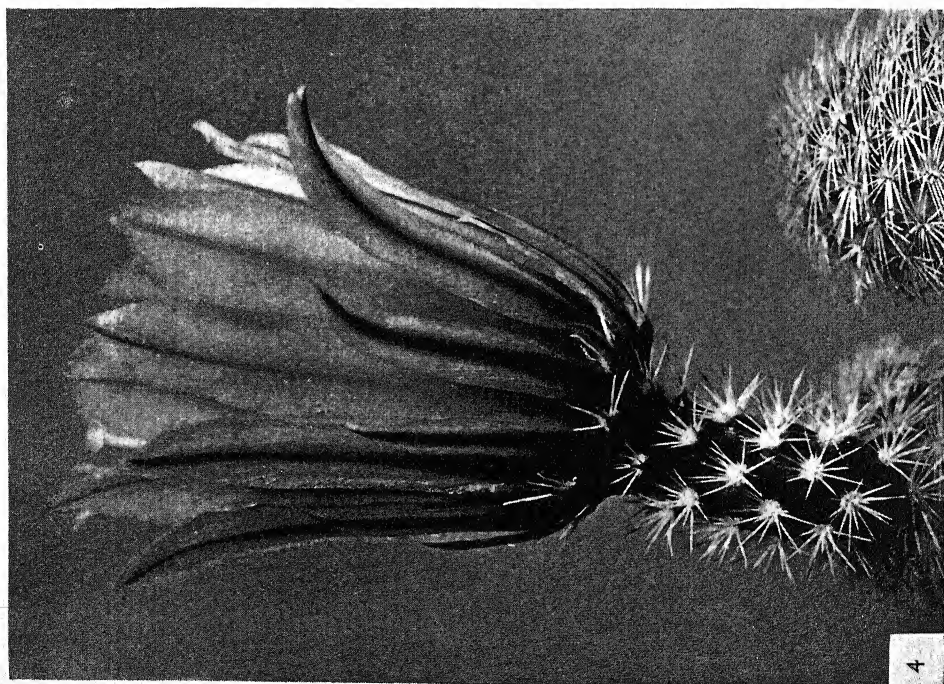
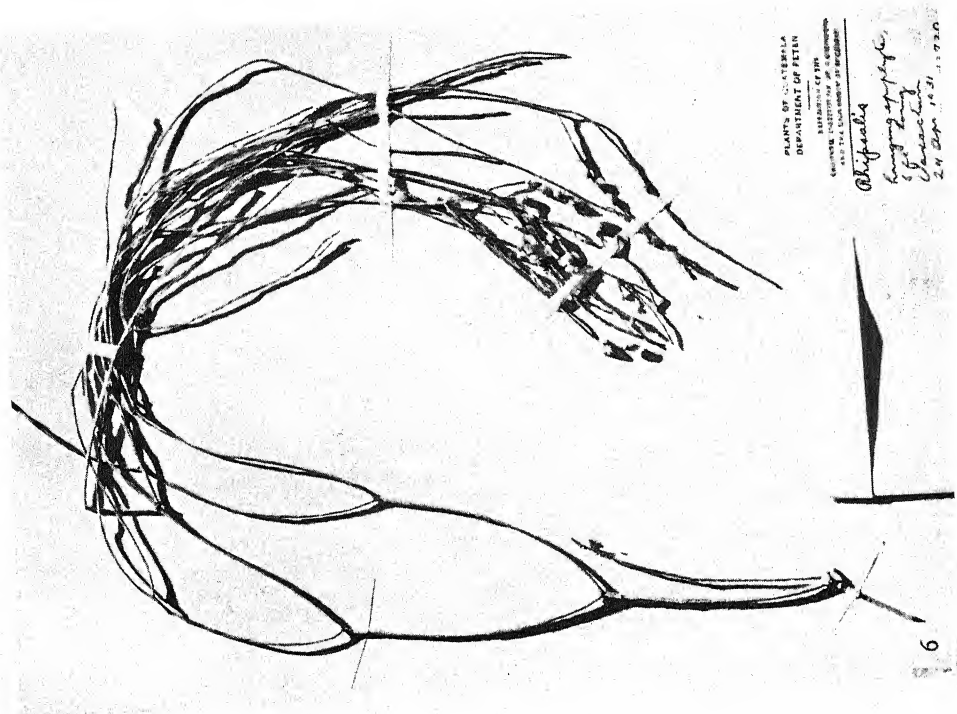
Fig. 5. *Deamia diabolica*.Fig. 4. *Echinocereus Steereana* in flower. (Slightly less than natural size.)



Fig. 7. Detail of same showing prominent areoles.

Fig. 6. Habit of *Rhipsalis Bartlettii*.

dense masses of tawny hairs, these 2–3 mm. long; flowering areoles not lanate, ovary sunken in the branch, fruit white, globose, 3–4 mm. in diameter; seeds black, reniform, less than 1 mm. long, testa reticulate furrowed. Flower unknown. Specimens were collected by H. H. Bartlett, Uaxactun, Petén, Guatemala, April 24, 1931. A single less ample specimen was collected for the University of Michigan Herbarium by E. Matuda at Cordoba, Vera Cruz, Mexico, August 14, 1936.

*Deamia diabolica* sp. nov. (fig. 5). Planta fruticulosa volubilis probabiliter ut in *D. Testudine* densissime epiphytica in arboribus humilibus prope litora, inferne ramosissimis, ramis radicantibus; costis 4–5 altissimis alatis, acutis, subcrenatis; spinis 12–20, dissimilibus, 5–52 mm. longis, acicularibus vel non-nihil triquetris, basi bulbosis, fuscis; floribus albis, 22–24 cm. longis tubo 9–11 cm. longo, setoso; ovario spinoso. Specimen typicum siccatum in Herb. Mich., Ann Arbor, Mich.

*Deamia diabolica* n. sp. (fig. 5). Stems robust, jointed, 3–4 angled, ribs thin and wing-like 3–4 cm. high, subcrenate, areoles on edges of wings 1.5–2 cm. across on mature stems; spines stout, various, 5–52 mm. long, brown, becoming grayish, bulbose at the base, acicular, terete to somewhat 3 angled, longer ones slightly curving, one spine in an areole often much longer than others; flower 22–24 cm. long, white, tube about 12 cm. long, bracts on tube small, areoles 1.5 cm. apart above, closer below, filled with tawny wool and usually 3 brown to yellowish, curling hairs 1–3 cm. long; inner perianth segments white, spatulate, apiculate, outer segments much shorter, linear greenish-white; style stout, extending beyond the stamens, stigma lobes 7; ovary ovate, densely spiny, spines golden-brown, acicular, interlocking, 3–5 cm. long, semi-rigid, areoles circular, filled with tawny wool; seeds about 2 mm. long, brown, shiny, subreniform, testa slightly reticulate. Specimens collected by Percy Gentle in the Corozal District, British Honduras, 1931–32. No. 490. Additional specimens were collected by Mercedes Aguilar La Libertad, Petén, Guatemala, June 7, 1934, no. 262.



## Notes on American melastomes, including nine new species

H. A. GLEASON

*Rhynchanthera paludicola* comb. nov. *Tibouchina paludicola* Donn. Sm. Bot. Gaz. 42: 293. 1906. In his original description the author mentioned the five sterile stamens and the slender beaks of the fertile anthers and remarked that these were abnormal characters for the genus. They are however perfectly normal characters for *Rhynchanthera*, section *Iso-stemones*. The species is related to *R. Hookeri* of the northern Andes, from which it differs in its larger flowers, much longer sepals, and the fewer and much longer glandular hairs of the hypanthium.

The only other North American species of the genus *Rhynchanthera* is *R. mexicana* DC., of southern Mexico and Panama. This is a member of the section *Anisostemones*, in which the connective of one stamen is greatly prolonged.

The genus *Centradenia* was credited with four species by Cogniaux in 1891. This number may now be increased to seven, all natives of the mountains and adjacent foothills of Mexico and Central America, extending south as far as Panama. The generic description given by Cogniaux needs a slight revision: the anthers are sometimes quite isomorphic; while often oblong or ovoid, as stated, they may also be linear-oblong or subulate, and in these narrower forms are acuminate.

Brandeggee's two species, *C. chiapensis* and *C. salicifolia*, are both valid and belong to the section *Eucentradenia*, characterized by strongly dimorphic anthers. *C. chiapensis* and *C. grandifolia*, with ebracteate flowers, glabrous hypanthium, and wide, strongly falcate leaves, are clearly related. In the latter the leaves are 4-nerved and the stem prominently winged; in the former the leaves are 3-nerved or 5-nerved and the stem merely 4-angled. *C. salicifolia* and *C. Bernoullii*, with glandular hypanthium and fairly broad leaves, are also related. In the latter the appendages of the larger stamens are terminated by two slender elongate lobes or setae, while in the former they are merely shallowly lobed.

In the section *Centradeniopsis*, characterized by stamens isomorphic or nearly so, a seventh species may now be described, differing from *C. floribunda* in its linear-subulate anthers with truncate appendages:

*Centradenia Maxoniana* sp. nov. Caules graciles, erecti (?), subflexuosi, subteretes, dense strigosi, pilis subulatis 0.6 mm. longis e basibus satis tumidis. Petioli foliorum majorum graciles, 2-5 mm. longi, strigosi. Laminae firmulae, supra virides, subtus pallidiores, lanceolatae, usque 10 cm. longae 2.2 cm. latae, acuminatae, integrae, paulo falcatae, basi inaequilaterales, latere uno longe cuneatae, altero obtusae vel rotundatae, 4-pli-nerviae, venis supra fere



planis subtus paulo elevatis, supra setosae, pilis gracilibus circa 0.5 mm. longis, subtus superficie glabrae ad venas strigosae, pilis rigidis 0.8 mm. longis. Folia minora subulata vel anguste lanceolata, 1–2 cm. longa, mox decidua. Cymulae 3–10-florae, caulem et ramulos ex axillis superioribus terminantes, pedunculis pedicellisque dense glanduloso-pubescentibus, pedicellis 3–5 mm. longis. Hypanthium anguste campanulatum, 8-costatum, 3.5 mm. longum, glanduloso-pubescentibus, pilis gracilibus adscendentibus 0.4–0.5 mm. longis, summo setis validioribus ornatum. Sepala triangularia e sinibus late rotundatis, 1 mm. longa, acuta, glabra vel fere glabra. Petala oblonga, 5 mm. longa, inaequilateralia, minute glanduloso-ciliata. Stamina isomorpha sed magnitudine inaequalia; filamenta 2–2.3 mm. longa; thecae lineari-subulatae, fere rectae, 2.8 vel 4 mm. longae, convolutae; connectivum brevissime productum, ad filamentum apicem oblique dilatatum, parte anteriore adscendente, quadrata, 0.5 mm. longa, parte posteriore descendente, ovata, 0.2 mm. longa. Ovarium obovoideo-oblongum, 2.8 mm. longum, glabrum; stylus gracilis, 6 mm. longus.

Type, *Pittier 5414*, collected between Hato del Jobo and Cerro Vaca, eastern Chiriquí, Panama, alt. 700–1000 meters, and deposited in the United States National Herbarium. Other specimens are *Williams 321*, from Panama; *Pittier 11061* and *Tonduz 7628*, from Costa Rica.

The genus *Chaetolepis* is primarily South American, with one species, *C. alpina* Naud., ranging north into Costa Rica. In western Cuba and the Isle of Pines the genus appears again, and from this rather restricted area Cogniaux recognized four species, *C. saturaeoides* Triana, *C. cubensis* Triana, *C. brevistrigillosa* Cogn., and *C. Grisebachii* Cogn. Careful examination of the ample material preserved in American herbaria has failed to disclose any reliable evidence which might indicate specific differences among them. They have been separated on such notoriously variable characters as the proportions and density of pubescence on the leaves, the shape and number of scales and hairs on the stem and hypanthium, the size and shape of the sepals, and the number of flowers, and in all of these features they intergrade freely. I therefore propose their union into a single species under the oldest specific name, *Chaetolepis cubensis* (A. Rich.) Triana.

The generic name *Heeria* was maintained by Triana and by Cogniaux because of its supposed priority of one year over *Heterocentron*, and in spite of the fact that *Heeria* was a later homonym. The next available name is apparently *Heterocentron*, which was used by Krasser and by Rose. Actually *Heterocentron* was published in 1838, a year earlier than *Heeria*, so that there can be no doubt of the proper name for this genus of Mexican and Central American plants.

Of greater importance is the possible segregation of the genus into two,

as was recommended by Rose, who very properly adopted *Schizocentron* Meissn. for the smaller group. In it the plants are decumbent or creeping, instead of erect, the flowers are solitary, instead of paniculate, and in the better known species the leaves are 3-nerved, instead of multipli-nerved. These characters give the plants an entirely different facies, but they are not supported by floral structures. In consistency with the standards used elsewhere in the family, the two groups must be kept within a single genus, as was done by both Triana and Cogniaux.

Cogniaux admitted six species in 1891. Since then four species have been added, *H. occidentalis* Rose in 1905, *H. suffruticosa* Brandg. in 1914, *H. alata* Rose & Standl. and *H. laxiflora* Standl. in 1924. I shall here describe four species as new, make two segregations from species previously recognized but recently united, and combine two old species into one, leaving the genus with fifteen species as recognized by me.

*Heterocentron subtripplinervia*, originally described by Link & Otto in the genus *Melastoma*, is the most abundantly represented species in most herbaria. In transferring the species to *Heterocentron*, Braun and Bouché noted that the difference between it and *H. rosea* was slight, the latter having an ovarial crown of four scales which was lacking in the former. Examination of an excellent series of specimens shows that this character is variable and that no other constant character can be found to separate them. *H. rosea* is accordingly reduced to synonymy.

The section *Euheeria* contained a single species, *H. elegans* (Schlecht.) Kuntze, in 1891. To this Brandegee added in 1914 an excellent species, *H. suffruticosa*, its hypanthium strigose with non-glandular hairs, rather than glandular-hirsute, and its leaves multipli-nerved, rather than 3-nerved. A third species of the group may now be described, agreeing with *H. elegans* in the characters above mentioned but differing in its sessile upper leaves and in its sepals exceeding the hypanthium.

***Heterocentron sessilis* sp. nov.** Fruticulus, caulibus gracilibus elongatis sarmentosis, subteretibus sed angustissime 4-alatis, sparse strigosis praesertim ad alas; internodia usque 5-10 cm. longa. Petioli graciles, 2-4 mm. longi, sparse strigosi. Laminae ovatae vel ovato-oblongae, 15-25 mm. longae 8-12 mm. latae, acutae, crenatae, ad basin late acutae usque rotundatae, 3-nerviae, supra et ad venas venulasque subtus sparse setosae, venis secundariis more Melastomatacearum nullis sed vena media venulas laterales curvatas emittenti; foliorum juga 1 vel 2 superiora sessilia, lata ovata, circa 8 mm. longa 5 mm. lata, basi rotundata vel subcordata. Flores solitarii, ramos laterales terminantes, pedunculis 2-3 cm. longis glabris gracilibus. Hypanthium campanulatum 4 mm. longum hirsutum, pilis patulis vel subreflexis 1.5 mm. longis basi incrassatis. Sepala erecta vel adscendentia, triangulari-lanceolata,

acuminata, minute ciliata, ceterum glabra, hypanthium paulo excedentia. Petala rubro-purpurea 10 mm. longa. Stamina modo generis. Ovarium apice glanduloso-setosum.

Type, *von Türckheim II 1554*, collected at Coban, Dept. Alta Verapaz, Guatemala, alt. 1550 meters, and deposited in the Gray Herbarium of Harvard University. *Von Türckheim 2470* in the Field Museum and the National Herbarium is the same. The type number in the Field Museum and the National Herbarium, *von Türckheim II 2364* in the same herbaria, and *von Türckheim 2471* in the National Herbarium represent an intermediate form between, and possibly a hybrid of, this species and *H. glandulosum* Schenck. They are characterized by paniculate flowers on short glandular pedicels and by larger leaves, many of which exhibit the multiple venation so characteristic of most species of the genus.

The remaining twelve species of *Heterocentron* may be divided into two groups, one of six species with glandular-hirsute hypanthium and one of five species with strigose non-glandular hypanthium, with a twelfth species of doubtful relationship.

In the first group two species are found in the western part of Mexico, in the states of Jalisco, Durango, Sinaloa, and Nayarit; in these the ovary is not setose at the summit. One of these, *H. mexicana* Hook. & Arn., the type of the genus, was combined by Cogniaux with *H. subtripplinervia*. Examination of original material shows that it is quite distinct. Related to it is an undescribed species, distinguished by glabrous and entire sepals, those of *H. mexicana* being glandular-ciliate and usually also pubescent on the back. It also differs in its larger panicle, its much larger flowers, and the stouter hairs of the hypanthium. This is:

***Heterocentron floribunda* sp. nov.** Caules erecti graciles, acute 4-angulati, 4-sulcati, tenuiter canescentes punctis minutis albis, internodiis glabris, nodis sparse setosis. Petioli graciles 5-10 mm. longi, sparse strigosi. Laminae tenues, ovato-ellipticae, pallide virides, 3-6 cm. longae 1.5-3 cm. latae, integrae, utrinque acutae, multipli-nerviae, jugis lateralibus 4 vel 5, supra et subtus ad venas sparsissime setosae, pilis gracilibus circa 0.5 mm. longis. Panicula elongata ramosa multiflora, ramis angularibus, sparse pubescens, pilis patulis circa 0.3 mm. longis, iis pedicellorum glandulosis; pedicelli supremi fere glabri, 5-8 mm. longi, bracteis 2 subulatis 1.5-2 mm. longis sustentis. Hypanthium late campanulatum, 4.3 mm. longum, pubescens, pilis patulis vel curvato-adscendentibus glandulosis 0.4-0.6 mm. longis, e basibus depresso-conicis 0.3-0.4 mm. altis. Sepala ovato-lanceolata vel triangularia, 5.5 mm. longa, basi 2.5 mm. lata, anguste acuminata, glabra, integra. Petala late obovata, 9 mm. longa 8 mm. lata, integra, venosa, conspicuiter inequilatera, vena media curvata. Filamenta gracilia, 4.5 vel 6 mm. longa; thecae 3.5 vel 4.6 mm. longae; connectiva staminum exteriorum paulo curvata, 2.7 mm. longa, infra

thecas paulo incrassata, appendice complanata, anguste clavata, obtusa, 2.4 mm. longa. Ovarium liberum glabrum; stylus sigmoideus 7 mm. longus.

Type, *Ortega 5329*, collected at Sianori, Durango, and deposited in the United States National Herbarium. Other collections, all from Durango, are *Ortega 4272*, *Palmer 102*, and *Rose 3509*.

The remaining four species in the group are natives of more southern regions, ranging from Jalisco to Costa Rica. Two of them, *H. glandulosa* Schenck and *H. axillaris* Naud., have glabrous entire sepals. They were united by Cogniaux, but may be distinguished specifically by the glandular-hirsute pedicels of the former and the strigose non-glandular pedicels of the latter.

The last two have glandular-pubescent, glandular-ciliate sepals. In *H. undulata* Naud. the setae of the ovary are non-glandular, the sepals are shorter than the hypanthium, and the connective of the longer stamens is half as long as its appendage. In the other, described below as new, the ovarian setae are glandular, the sepals exceed the hypanthium, and the connective is longer than the appendage.

***Heterocentron salvadorana* sp. nov.** Suffruticosa, 1 m. alta, caulibus acute 4-angulatis, supra tomentulosis, demum glabrescentibus. Petioli 5-8 mm. longi. Laminae firmulae, ovato-ellipticae, 3-7 cm. longae 2-3 cm. latae, obtusae, integrae, basi late cuneatae, multipl-nerviae, utrinque tenuiter pubescentes. Panicula magna multiflora, pedicellis brevibus dense glandulosis. Hypanthium subglobosum, 2.8 mm. longum, dense glanduloso pubescens, pilis patulis 0.3 mm. longis. Sepala ad anthesin reflexa, ovata, 3.2 mm. longa, basi 2.2 mm. lata, apice involuta, glanduloso-ciliata, ciliis 0.1 mm. longis, glanduloso-pubescentia. Petala late obovata, 5 mm. longa 4 mm. lata, glanduloso-ciliata, pilis 0.1 mm. longis. Filamenta 4 vel 5.5 mm. longa; thecae 2.8 vel 3.5 mm. longae; connectivum staminum majorum supra filamentum fere rectum 2 mm. longum, infra filamentum in calcar 2 subulata divisum. Ovarii squamae semicirculares erectae, 0.4 mm. altae, densissime glanduloso-ciliatae, pilis fere contiguis, usque 0.8 mm. longis, fructu persistentibus.

Type, *Standley 20398*, collected at Santa Ana, Dept. Santa Ana, Salvador, and deposited in the United States National Herbarium.

Recent collections from Chiapas have disclosed a fourth undescribed species, marked by excellent morphological characters but of doubtful relationships. This is:

***Heterocentron muricata* sp. nov.** Caulis partes superiores acute 4-angulatae, glabrae vel levissime strigosulae, ad nodos dense breviterque barbatae. Laminae membranaceae, oblongae, 2-4 cm. longae, 1-2 cm. latae, breviter abrupteque acuminatae, ad basin late cuneatae in petiolum brevem superne alatum, supra minutissime strigosulae, subtus sparse strigosae, praecipue ad

venas. Ramuli floriferi ex axillis superioribus divaricati, pauciflori, superne strigosi; pedicelli veri 4-8 mm. longi gracillimi glabri. Hypanthium subgloboseum, 4.5 mm. longum, valde muricatum, muricis ca. 1 mm. longis, ceterum glabrum. Sepala anguste triangularia 6.5 mm. longa, ad anthesin reflexa, nunc integra, nunc brevissime sparseque ciliata. Petala staminaque non visa, sed connectivum unum 1.9 mm. longum alte bilobum, anthera unica 2.6 mm. longa. Ovarium apice squamis 4 quadrato-ovatis glanduloso-ciliatis coronatum; stylus gracilis sigmoideus 8 mm. longus, stigmatе punctiformi.

Type, *Matuda* 1967, collected at Montecristo, Chiapas, January, 1938, without further data, and deposited in the Britton Herbarium at the New York Botanical Garden. Although in general habit our plant somewhat resembles *H. suffruticosa* Brandg., also from Chiapas, it differs notably in its muricate hypanthium and its squamiferous ovary. The latter feature indicates a possible relation to the group of five species mentioned previously, including the common *H. subtripplinervium* A. Br. & Bouché, but none of this group has a muricate hypanthium. Stoutly subulate hypanthial hairs are characteristic of *H. undulata* Naud., but in that species glandular pubescence is abundant, the hypanthium is much smaller, and the sepals only 2-2.5 mm. long.

David Don established the genus *Arthrostemma* in 1823, crediting it to Pavon, and including five species which are now assigned to three different genera in as many different tribes of the family. As a result, it accumulated many unrelated species during the next fifty years, and several of its species were segregated under various generic names. Triana accepted the genus in the sense of Ruiz and Pavon in 1871 and it was so continued by Cogniaux in 1891. Three North American species were recognized by Cogniaux, *A. fragile* Lindl., *A. campanulare* Triana, and *A. parvifolium* Cogn.

The characters of the genus, as regularly understood since the work of Triana, are definite. The flowers are 4-merous, with slender elongate hypanthium and short triangular sepals; petals large, fugacious or caducous; stamens dimorphic; anthers linear; connective conspicuously prolonged below the thecae, bearing a large anterior appendage, 2-3-toothed or lobed at its apex; ovary free, 4-celled.

Triana described *A. alatum* in 1871 from Venezuelan material without flowers. Flowering specimens are now available from Panama and Salvador and show that the anthers are nearly isomorphic, quite small, ovoid in shape, with a very short connective bearing a subulate spur. Notwithstanding these discrepancies, the plant is obviously a good *Arthrostemma*, and the generic description must be revised accordingly.

Cogniaux described *A. parvifolium* from Guatemalan material without flowers, and in 1904 Donnell Smith described *A. apodocarpum* from the



same country. Comparison of the types shows that these two species are identical. Smith dismissed the structure of the anthers in five words, "stamina parva inaequalia" and "antheris parvulis." Here also they are short, ovoid in shape, nearly isomorphic, with a short connective bearing a flat truncate spur. Clearly *A. alatum* and *A. parvifolium* are closely related. In the latter the leaves are acute to cuneate at the base and the filaments are glandular-pubescent; in the former the leaves are rounded to subcordate at the base and the filaments are glabrous.

*A. hirtellum* Cogn. was described from Guatemalan material in fruit. So far as known to me, it has been collected but once and I have seen three specimens of this type collection. Flowers are absent, although Cogniaux describes the anthers in terms that might well apply to an *Arthrostemma*, but without stating dimensions or proportions. The plant differs notably from all other species of the genus in its short, broadly campanulate hypanthium, its elongate sepals, and its setose ovary, and there can be little doubt that it is not an *Arthrostemma*. Its generic affiliation cannot be settled until flowering material can be examined.

The well known name *Arthrostemma campanulare* Triana (1871) is not tenable, being a later homonym antedated by *Arthrostemma campanulare* DC. (1828). It has been replaced by *A. macrodesmum* Gl.; Williams, Fl. Trin. & Tob. 356, 357. 1934.

The genus *Monochaetum* is represented in North America by seventeen species, all montane or subalpine in their distribution. Two of these are known only from recent collections and are described below. They suggest that further exploration in the less accessible mountains of Central America may reveal still other species.

***Monochaetum compressum*** sp. nov. Frutex ramosissimus usque 2 m. altus, caulibus gracilibus hirsutulis, pilis e basibus papillois leviter retrorsis, internodiis 5–10 mm. longis. Petioli 1–3 mm. longi patentim hirsuti. Laminae firmulae oblongae vel oblongo-lanceolatae, 5–17 mm. longae 3–6 mm. latae, acutae vel obtusae, integrae, basi obtusae vel rotundatae, levissime 3-plicatae, nerviae, supra virides sparse strigosae, venis primariis leviter impressis, secundariis obsoletis, subtus pallidae molliter villosae, venis secundariis obscuris reticulatis. Flores solitarii, ramulos breves terminantes, pedicellis hirsutis, quam hypanthio brevioribus. Hypanthium fusiformi-campanulatum 8–9 mm. longum, sparse hirsutum, pilis eglandulosis patulis 0.6–0.8 mm. longis e basibus papillois. Sepala patentia oblongo-triangularia, 5.6 mm. longa 2.4 mm. lata, ciliata, dorso sparse hirsuta, pilis non papillatis. Petala pallide purpurea circa 15 mm. longa. Stamina interiora: Filamenta 10 mm. longa; antherae erectae subulatae 6.2 mm. longae; appendices adscendentes oblongae 3.3 mm. longae. Stamina exteriora: Filamenta 9 mm. longa; antherae arcuatae 9–10 mm. longae; appendices 5 mm. longae dorso alte canaliculatae, lateribus

adpressis. Ovarium summo villosum, pilis erectis 0.9 mm. longis; stylus 7.5 mm. longus.

Type, *Skutch 1516*, collected on the south slope of Volcano Atitlan, Dept. Suchitepequez, Guatemala, alt. 2400 meters, and deposited in the Britton Herbarium at the New York Botanical Garden. In its freely branched stem and small leaves, *M. compressum* has a superficial resemblance to *M. Deppeanum* Naud. It differs from that species in its larger anthers and in the shape of its anther-appendages. These features, together with its large flowers and papillate pubescence of minutely barbellate hairs, indicate its relationship to *M. macrantherum* Cl. It is distinguished from this species by its hirsute pubescence on stem and hypanthium and by its 3-ply-nerved leaves which are uniformly pubescent on both sides.

***Monochaetum rubescens* sp. nov.** Frutex parce ramosus, caulibus praeter nodos minutissime setosos glabris rubescentibus. Petioli graciles 5–10 mm. longi glabri. Folia membranacea ovato-lanceolata vel ovata, maxima usque 42 mm. longa 19 mm. lata, superiora minora, acuminata, minutissime serrulata, dentibus seta adpressa brevi terminatis, basi acuta vel abrupte cuneata, 3–5-ply-nervia, supra opaca vel rubescentia, glabra, venis primariis angustissime impressis secundariis obsoletis, subtus pallida sparsissime setosa, venis primariis leviter elevatis, secundariis obscuris flexuosis. Flores 1 vel 3, caulem et ramos 2 supremos terminantes, pedicellis quam hypanthio dimidio brevioribus glabris. Hypanthium campanulatum rubro-purpureum 7 mm. longum, glabrum praeter setas paucas breves terminales. Sepala patentia rubro-purpurea oblongo-ligulata 7.5 mm. longa 3 mm. lata, acuta, ciliata, setis 1–3 ornata ceterum glabra. Petala purpurea late obovata 20–25 mm. longa. Stamina interiora: Filamenta complanata 10 mm. longa; antherae erectae subulatae 4.4–4.7 mm. longae; appendices curvato-erectae anguste ellipticae 4 mm. longae 0.9 mm. latae. Stamina exteriora: Filamenta 8.5 mm. longa; antherae arcuatae circa 10 mm. longae; appendices ad apicem dilatatae teretes 5 mm. longae. Ovarium ad apicem sparse setosum; stylus glaber 7.5 mm. longus.

Type, *Matuda 0932*, collected at Siltepec, Chiapas, and deposited in the herbarium of the University of Michigan. *Matuda 1015*, from Mt. Pasitar, Chiapas, agrees with the type in every detail. *Matuda 0973*, from Mt. Orando, Chiapas, has somewhat longer leaves, reaching 60 mm. in length and only 20 mm. in width. The few-flowered inflorescence, the almost complete absence of pubescence, and especially the terete appendages of the larger anthers indicate that *M. rubescens* belongs to the species-group

<sup>1</sup> Am. Jour. Bot. 16: 586–594. 1929.

Pringleae.<sup>1</sup> The three (or possibly four) species hitherto known have shorter sepals and conspicuously strigose or glandular hypanthia.

The huge genus *Miconia*, already with nine hundred described species, continues to receive additions in many parts of its range. The two described below are both well marked and abundantly distinct from the species hitherto known.

*Miconia filamentosa* sp. nov. Sect. *Eumiconia*: arbuscula; rami superiores teretes graciles, tenuissime stellato-puberuli, internodiis 3–8 cm. longis. Folia in quoque jugo subaequalia. Petioli 2–5 mm. longi, minute stellato-puberuli. Laminae tenues oblongae vel oblongo-lanceolatae vel anguste lanceolatae, usque 12 cm. longae 3 cm. latae, anguste acuminatae, conspicue obcrenatae, ad basin minute cordulatam angustatae, 3-nerviae vel fere 3-plici-nerviae, supra glabrae, subtus ad venas sparsissime stellato-puberulae, venis secundariis 2–3 mm. dissitis sub angulo 80° divergentibus. Panicula terminalis, 6–8 cm. longa lataque, ubique densiuscule stellato-puberula, ramis oppositis divaricatis, ad nodos omnes lineari-bracteolata, bracteolis 0.8 mm. longis. Flores 5-meri, sessiles in cymulis trifloris sed flores laterales ut videtur pedicellati. Hypanthium obconicum, ad torum 1.8 mm. longum, stellato-puberulum. Calycis tubus nullus vel usque 0.2 mm. longus, sepalis e sinibus acutis semicircularibus vel triangularibus, 0.5 mm. longis, rotundatis vel acutis, minutissime ciliatis, dentibus exterioribus crasse conicis. Petala anguste obovato-oblonga, 3 mm. longa 1.3 mm. lata, glabra, paulo retusa. Stamina dimorpha. Filamenta gracillima, 4.6 vel 2.3 mm. longa. Antherae lineares, 3 vel 2.3 mm. longae, poro terminali latiusculo dehiscentes. Connectivum staminum majorum infra thecas 0.7 mm. productum et in lobum obliquum rotundatum, filamentum fere amplectentem expansum, staminum minorum 0.4 mm. productum et in lobum 1 rectum dorsalem et lobos 2 laterales deflexos divisum. Ovarium seminferum, 4-loculare, summo rotundatum, minute pubescens, obscure 10-lobatum, ovulis in quoque loculo circa 8; stylus gracilis glaber, 5.5 mm. longus; stigma minute capitatum.

Type, *Klug 938*, collected at Mishayacu, near Iquitos, Dept. Loreto, Peru, in forest at an altitude of 100 meters, and deposited in the Britton Herbarium at the New York Botanical Garden. In *Williams 3306*, a fruiting specimen with less crenate leaves and a panicle up to 20 cm. long, the fruit is spherical and about 2 mm. in diameter. In *Krukoff 8936*, from São Paulo de Olivença, Brazil, the flowers and pubescence are essentially identical with the type, but the leaves are much broader at the base and deeply cordate, consequently appearing subsessile. *M. filamentosa* has been compared with practically every described species of the section. It is probably nearest to *M. Sprucei* Triana, in which the leaves are much wider, more abruptly acuminate, essentially entire, and entirely lacking the heart-shaped base.

***Miconia incurva*** sp. nov. Sect. *Amblyarrhena*: frutex 9 m. altus, caulibus, petiolis, foliorum pagina inferiore, inflorescentia, hypanthiis, et calycibus ferrugineo-stellato-tomentosis. Rami graciles demum glabrescentes, internodiis 1–2 cm. longis. Petioli satis graciles 5–10 mm. longi. Laminae tenues, oblongo-lanceolatae, maximae 13 cm. longae 3.5 cm. latae, anguste acuminatae, integrae, basi obtusae vel late acutae, 3-ply-nerviae ca. 1 cm. supra basin, supra glabrae; venae primariae supra impressae, submarginalibus validis, secundariae 2–3 mm. dissitae, sub angulo fere recto divergentes. Paniculae ca. 5 cm. longae lataeque, ramis oppositis; bractae persistentes triangulari-subulatae 2–4 mm. longae; cymulae triflorae. Flores 5-meri. Hypanthium obconicum carnosum, ad torum 6.7 mm. longum, intus obscure costatum. Calycis tubus fere erectus, 3.3 mm. altus, lobis brevissimis truncatis subscariosis, margine libero fere nullo, dentibus exterioribus flexuosis incurvis subulatis 7 mm. longis. Petala alba, late obovata, valde obliqua, basi subunguiculata, 10–11 mm. longa lataque. Stamina isomorpha; filamenta glabra 5.5 mm. longa, medio leviter dilatata, infra antheram subito contracta; antherae oblongae, 4.7 mm. longae, 2-loculares, poro minuto ventrali-terminali dehiscentes, connectivo incrassato non producto. Ovarium inferum 5-loculare, summo concavo circum stylum annulato; stylus crassus teres 14 mm. longus, stigmate capitato subgloboso, 2 mm. diametro.

Type, *Skutch 3273*, collected at Vara Blanca de Sarapiquí, north slope of Central Cordillera, Costa Rica, alt. 1500–1700 meters, and deposited in the Britton Herbarium at the New York Botanical Garden. While the plant is obviously a *Miconia*, with anthers externally resembling the typical form of the section *Amblyarrhena*, it is exceptional for the section in having only two loculi in the anthers. Very few species of the section have elongate exterior teeth, and they differ notably in other structural features.

NEW YORK BOTANICAL GARDEN.

## INDEX TO AMERICAN BOTANICAL LITERATURE 1935-1937

The aim of this Index is to include all current botanical literature written by American, published in America, or based upon American material; the word America being used in the broadest sense.

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## Some Psilophytales from the Hamilton group in western New York<sup>1</sup>

CHARLES B. READ  
(WITH PLATE 30)

### INTRODUCTION

In the spring and early summer of 1936, Mr. Carl W. Mumm and the writer spent six weeks collecting fossil plants in the Devonian sections of western New York from Canandaigua Lake westward to Lake Erie in the vicinity of Buffalo. Particular attention was given to the thin, lenticular masses of iron pyrites which occur in many localities at the top of the Moscow shale of late Hamilton age and below the Genesee shale of early Genesee age. Because this ferruginous band has been regarded in the past as the thin western representative of the Tully limestone it is known as the Tully pyrites. In recent years it has been assigned to the Hamilton by Cooper and Williams (5). The general features of these beds are well-known to geologists. They occur as lenses which may be 6 to 8 inches thick and have an areal extent of several hundred square feet. Upon close examination, the material is seen to consist of the pyritized remains of a varied, dwarfed marine fauna intermingled with rare fragments of fossil plants. Small quantities of calcium carbonate remain, but the fossils are largely infiltrated and replaced by the sulphide of iron which likewise acts as a cementing agent. Evidently the pyrites band marks a shoaling of the Devonian seas and probably development of shallow lagoons of small extent where the marine fauna lived under conditions which caused its dwarfing. Land vegetation must have been established in areas near enough so that occasional fragments could drift in and become entombed on the foul bottom where they were preserved by infiltration of iron sulphide.

For the most part, the plant fossils consist of bits of stems and petioles which, in some cases, were crushed before petrification. The flattened specimens are, of course, very difficult to work with. However, those which are uncrushed or only partly flattened in many cases reveal sufficient detail to permit morphological study. Owing to the opaque nature of the iron pyrites the sections must be cut and polished for study with reflected light rather than ground thin for transmitted light.

The majority of the specimens collected are yet unstudied, except in a very preliminary fashion. The flora is, however, of fair size for such an early one and promises to furnish considerable information bearing on the

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morphology of the Devonian plants. Two of the forms present are members of the Psilophytales and are extremely interesting—one because of the fact that it is the second record of the genus, which has been previously known only from Middle Devonian rocks in the Burdeck Basin, Queensland, Australia, and the other because of its possible bearing on the relationship of the Psilophytales and the early fernlike types.

There follow brief preliminary descriptions which point out the principal features of these forms.

PSILOPSIDA  
PSILOPHYTALES  
ASTEROXYLEAE

**Schizopodium mummii, n. sp.**

In the suite of specimens collected in Gooding's Landing Ravine near Cottage City and a mile or so from the shore on the east side of Canandaigua Lake is a block carrying a fragment of a stem which is referable to the genus *Schizopodium* Harris (7), previously known only from a single specimen collected in rocks of Middle Devonian age in Australia. The general aspect of this plant, which has been named for Mr. C. W. Mumm of the Geological Survey, is seen in figures 1-3. It will be observed that the fossil consists of a stem fragment carrying a lobate stele roughly cross-shaped in outline but with the ends of the bars enlarged as a result of the formation of a sort of secondary xylem. Surrounding this stele are bits of parenchyma, but in general these outer tissues are very poorly preserved and provide little morphological information of value.

A more detailed examination of the xylem reveals the fact that this is for the most part clearly primary. There appears to be an enlarged area of this tissue towards the extremity of each arm. Apparently, these arms become complicated as a result of further splitting or fluting of the column, as is seen in figures 2 and 3. The position of the protoxylem is definitely mesarch, a feature which is particularly obvious in figure 1. The most striking feature of this fossil is the development of what appears at first glance to be secondary growth at the apices of the arms or lobes of the column of xylem. This regular radially directed xylem is seen at xr in figure 1 as well as in the other two figures taken at lower magnifications. The preservation of the outer tissues is unfortunately so poor that cambium, if originally present, cannot be seen.

In the very similar tissue observed in the Australian *Schizopodium davidi*, Harris was of the opinion that this is not a true secondary xylem, since he could find no trace of cambium even in well-preserved specimens. He was, rather, of the opinion that this was a sort of pseudo-secondary

xylem. In discussing the probable origin of this radially arranged wood which he regarded as intermediate between true secondary and primary xylem, he suggested that "the desmogen cells outside the protoxylem tend to divide radially, which is the one direction in which they can divide freely, while the inner desmogen cells divide irregularly" (7). Thus, the irregularly as well as the radially arranged xylem could have been developed.

As regards the pitting of the tracheids, in the small amount of material at hand it has been impossible to demonstrate this. In *Schizopodium davidi* the pitting was shown to be scalariform in the protoxylem and multi-seriate-bordered in the metaxylem and the problematical secondary growth.

Summarizing the information, *Schizopodium mummii* is known at present from a fragment which indicates a slender axis carrying a solid xylem strand cross-shaped in transverse section. Presumably, the phloem followed its contour. The apices of the lobes are marked by the occurrence of a somewhat radially arranged xylem presenting the appearance of being secondary. The exact nature of this tissue cannot be determined from this material owing to its poor preservation.

*Schizopodium mummii* appears to be quite closely related to *S. davidi* Harris (7). However, an important difference is seen in the definitely mesarch nature of the primary xylem (excluding the radially arranged tissue) in the American plant as opposed to the exarch condition in the Australian specimen. Comparisons, however, cannot be carried very far at present owing to the fragmentary nature of the material.

The most interesting fact about this plant is its presence in Middle Devonian (Hamilton) strata of New York, some 9,000 miles from Queensland, Australia, where the only other known species of the genus is found, also in rocks of Middle Devonian age (7). This may be taken to indicate that the genus is widely distributed, and was a frequent type in the Devonian landscape. It seems almost certain that it will be found at numerous localities as the Devonian floras are more completely studied.

*Locality*.—Outcrop known locally as Tully pyrites at stream level in Goodings's Landing Ravine, 1 mile east of Gooding's Landing, Canandaigua Lake, New York.

#### ARACHNOXYLON n. gen.<sup>2</sup>

Characters at present are those of the only known species, which follows.

<sup>2</sup> From the Greek *ἀράχνη*, spider, and *ξύλον*, wood, having reference to the outline of the xylem as seen in transverse section.



**Aarchnoxylon kopfi (Arnold), n. comb.**

*Asteropteris kopfi* Arnold, Buffalo Soc. Nat. Sci. Bull., 17 (1): 7-9, text fig. 2.

In 1935 Arnold described, under the name *Asteropteris kopfi*, a poorly preserved fragment of a small stem, the only illustration being a diagram. It is clear, however, from his description that he had in hand a specimen identical with the splendidly preserved stem in the writer's more recent collection from Canandaigua Lake. As will be shown at a later point, this species is not congeneric with *Asteropteris* Dawson and must be assigned to a new genus.

The general features of *Arachnoxylon kopfi* are shown in figure 4, which is a photograph, of a polished surface of a transverse section, magnified about 10 times. In the center is a highly fluted strand of xylem appearing as a many-armed, starlike figure. Near the apex of each of the protuberances is situated the mesarch protoxylem and a small island of parenchyma which usually is disorganized. The exact situation is perhaps made somewhat clearer by an examination of figure 5, which is a photograph taken at somewhat higher magnification. The protoxylem is centered around an area of what was apparently undifferentiated parenchyma forming a so-called loop. This is a structure which is rather characteristic of the early ferns.

Sheathing the xylem is parenchyma which is probably referable to phloem, and which appears to follow the contour of the xylem in a general way, although there is much greater thickness in the reëntrants or bays than there is in the region of the apices. The dark spaces shown in this tissue are simply cavities or holes where the pyrites has been dragged from the interior of cells. In the oblique light used to illuminate the surface these, owing to the shadows which are cast, appear as dark cells suggesting gum-filled spaces. The details of this tissue cannot be made out, although its limits are clear.

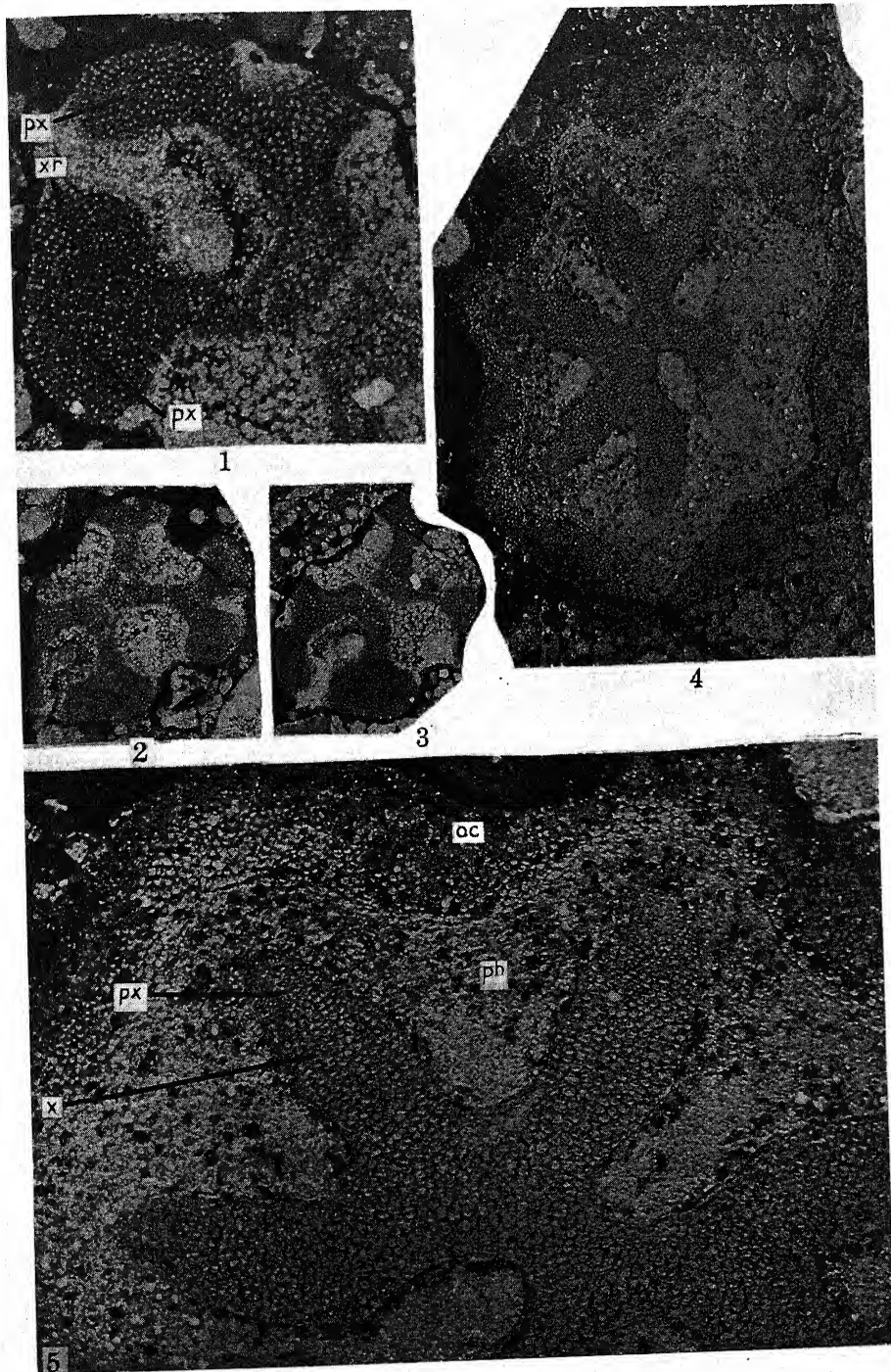
On the exterior is small-celled parenchyma forming a zone of ap-

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**Explanation of Plate 30**

Figs. 1-3. *Schizopodium mummii* n. sp. Figs. 2 and 3 transverse sections of the stem illustrating the lobed outline of the xylem and showing the enlarged apices of the arms  $\times 10$ ; Fig. 1 a portion of a stem at a somewhat higher magnification showing the protoxylem (*px*), the metaxylem, and the radially directed xylem (*xr*),  $\times 25$ .

Figs. 4, 5. *Arachnoxylon kopfi* (Arnold) n. comb. Fig. 4 transverse section of the stem showing the stellate xylem, the problematical phloem, and the general relations of the tissues  $\times 10$ ; Fig. 5 portion of the same section at a higher magnification, (*x*) the metaxylem, (*px*) the protoxylem, (*ph*) the problematical phloem, (*oc*) the cortex,  $\times 25$ .



READ: PSILOPHYTALES

preciable width and extending outward as far as the present limits of the specimen. This is probably cortex and extends just under the epidermis.

Noteworthy is the fact that there are no vascular strands given off by the stem stele and passing out into leaves. It is, of course, possible that there may have been scale leaves, but there is no evidence of any larger leaves with vascular tissue.

In summary, then, the stem of *Arachnoxylon kopfi* presents the following features:

1. A stele stellate in transverse section with a solid xylem and sinuous xylem arms. In other words, it is a highly fluted column. The xylem is mesarch, a protoxylem group being situated at the apex of each arm. An island of parenchyma occupies the middle of each protoxylem group. The phloem follows the xylem contours but fills to a greater extent the bays than the points, thus making less prominent the fluted nature of the stele.

2. On the exterior is a small-celled parenchyma extending to the outer edge of preserved material.

3. Leaf traces or other vascular strands are not known to depart from the stele, and there is no evidence of leaves of any sort existing. Branching is unknown.

From the above description it is evident that the New York fossil approaches representatives of the genus *Asteroxylon* in general organization. Both have a stellate xylem, and the zone of phloem is similar in both cases. In the known species of *Asteroxylon* (8, 9, 10) the protoxylem is slightly immersed but does not form the prominent loops that are seen in *Arachnoxylon kopfi*. It is impossible to compare the leaves or scalelike emergences in the two since there is no evidence of such structures in *A. kopfi*. The great difference between *Asteroxylon* and *Arachnoxylon* is the presence of the mesarch protoxylem and the parenchymatous island or peripheral loop in the apex of each arm in the latter, as opposed to the very simple, slightly immersed protoxylem area in *Asteroxylon*. Examination of the material also gives the impression that there is more of a fixity in the stelar form in *Arachnoxylon* than in the *Asteroxylon*. In the writer's opinion the presence of this "peripheral loop" is a matter of considerable importance.

The reasons for removing the fossil under discussion from *Asteropteris* Dawson are rather obvious. The two are quite different. *Asteropteris novaboracensis* (3, 6), the only known species, is a siphonostelic stellate type which shows evidences of whorls of phyllophores. The features of both stem and phyllophore trace indicate its inclusion in the Zygopteridaceae. Apart from the occurrence of "peripheral loops" in the arms of both there is no more than a very general similarity of stelar form.

This fossil, *Arachnoxylon kopfi*, seems to represent a very important morphological type among Devonian plants. From the viewpoint of stem structure it is rather close to what might be considered the fern prototype. It is a nonmedullated stellate type, a protostele approaching in form the stellate steles of the Devonian and Carboniferous Zygopterideae, such as *Asteropteris novaboracensis* Dawson, *Ankyropteris grayi* (Williamson) Scott, *Ankyropteris henricksi* Read, *Austroclepsis osborni* Sahni, and *Asteroclaena laxa* Stenzel. The protoxylem, it will be recalled, is situated around the "peripheral loops" of undifferentiated parenchyma in these ferns and presents an appearance identical to the mesarch condition observed in *Arachnoxylon*. The writer is of the opinion that this is an indication of real relationship. It is true that the zone interpreted as phloem is quite broad in the New York plant as compared with the similar tissue in the Zygopterideae. However, this is only a matter of detail and could readily have been modified. With increase in size such a plant type might readily have developed a parenchymatous central area in the stele constituting a mixed or true pith. And from the dichotomous or lateral branches of such a type one might expect to develop the primitive tetrastichous phyllophore which is characteristic of *Asteropteris novaboracensis* or the structure typical of *Stauropteris* (1, 2), the earliest members of the Zygopterideae whose stelar morphology is well-known.

In short, the writer suggests that such a type as *Arachnoxylon kopfi* may be regarded as morphologically close to the psilophytelean ancestor from which the Paleozoic fern types were derived. The peripheral loop points to a certain amount of relationship between the Zygopterideae and the fossil described above. From such stelar type the phyllophore of the *Stauropteris* or *Asteropteris* type could have readily been derived as a result of branching.

It is likewise probable that from a type showing the structural features of this plant the Cladoxyleae were derived as a result of stelar branching, resulting in the so-called polystelic condition, a factor related to increase in size, and at the same time modification of lateral branches into megaphylls. This group, the Cladoxyleae, still is problematical, although Bertrand (4) has gone far toward its elucidation. In his opinion its affinities lie with the ferns.

*Locality*.—Outcrop known locally as Tully pyrites at stream level in Gooding's Landing Ravine, 1 mile east of Gooding's Landing, Canandaigua Lake, New York.

#### SUMMARY

1. Two representatives of the Psilophytales are described from the



upper Middle Devonian of western New York. These are *Schizopodium mummii* n. sp., and *Arachnoxylon kopfi* (Arnold) n. comb.

2. *Schizopodium mummii* is a stellate type showing a small amount of radially arranged, secondary-like xylem at the apex of each arm. The type specimen is only a fragment. This fossil is the second known occurrence of the genus, the other station being in Queensland, Australia, in rocks of approximately the same age as those in which *S. mummii* occurs.

3. *Arachnoxylon kopfi* (Arnold) n. comb., is a form resembling known representatives of the genus *Asteroxylon*. It differs in its more robust aspect and in the presence of loops or islands of parenchyma around which is located the protoxylem near the apex of each arm. The phloem loosely follows the contour of the xylem, and outside is a zone of parenchyma. Appendages, and branches are unknown.

4. It is suggested that from a plant showing stem structure similar to *Arachnoxylon* the early fern types such as the Zygopterideae and the Cladoxyleae may have been derived. The writer is inclined to regard this form as highly organized representative of the Psilophytales "on its way towards becoming a fern."

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## Notes on plants of the Pacific Islands. I.

F. R. FOSBERG

To record miscellaneous and fragmentary observations accumulated while studying and determining plants from various islands of the Pacific it seems worth while to start a series of papers, to appear at irregular intervals as sufficient material accumulates. The first of these is presented here, treating species of the genera *Gouania* (Rhamnaceae), *Diospyros* (Ebenaceae), and *Randia* (Rubiaceae).

Thanks are due to the authorities and staff of the New York Botanical Garden for the privilege of working in the herbarium and for various courtesies extended to me while working there, and also to the authorities of the Bernice Pauahi Bishop Museum, of Honolulu, for the loan of some of the specimens treated in this paper.

### GOUANIA

*Gouania mangarevica* Fosberg, n. sp. Frutex scandens hirsutus vel tomentosus, folia dimorpha piloso-hirsuta supra bullata serrata membranacea vel chartacea, flores in spicas glomerata, spicae maxime 12 cm. longae, bracteoli minuti caduci, flores maxime 3 mm. latae pentameræ, styli 3, discus sub stylis barbatus in lobos triangulares productus.

Liane 20 m. or more long, older parts woody, younger parts hirsute-pilose with tawny spreading hairs, older parts becoming rusty-tomentose; leaves alternate, dimorphic, sparsely hirsute-pilose on both sides, especially beneath on the veins, bullate above, those on young sterile parts of the plants oblong or oblong-ovate, up to 9 cm. long and 4 cm. wide, truncate at base, acuminate at apex, coarsely serrate, especially above, membranous, those on older parts broadly ovate- or elliptic-cordate, obtuse to acuminate, usually shorter than those on sterile branches, as much as 6 cm. wide, chartaceous; tendril-bearing branchlets in the axils of the leaves, these sometimes bearing one or two small leaves, the tendrils slender on young branches but becoming much thickened and woody on the older parts, 2-3 tendrils borne on one branchlet, on older parts these branchlets more robust, sometimes occurring 2 at one node, bearing the inflorescences as well as tendrils. Inflorescence densely yellowish-tomentose, spicate; spikes as much as 12 cm. long, often borne as many as 6 on a branchlet, forming a panicle; glomerules small, subtended by minute caducous bractlets, often scarcely manifest; flowers usually sessile, rarely short-pedicelled, pentamerous, about 3 mm. across when spread out; calyx tomentose externally, its lobes ovate, 1 mm. long, obtuse, glabrous within; petals alternate with the calyx lobes, clawed at the base, about 1 mm. long, the limb suborbicular, saccate, surrounding the upper part of the stamen; stamens opposite and almost equalling the petals; filaments flat, dilated toward the base, inserted beneath the disk between its lobes; anthers almost

circular, 0.2–0.3 mm. long, the anther sacs terete; disk thin, produced into triangular lobes with strap-shaped apices, opposite the calyx lobes and two-thirds their length, glabrous except for a conspicuous tuft of hair immediately below the styles; styles 3, distinct to the base, divergent, glabrous, fleshy, about 0.7 mm. long; ovary inferior but indistinct in flower; fruit unknown.

GAMBIER ISLANDS, MANGAREVA: South side Mt. Mokoto, upper forest' climbing over bushes and trees, alt. 320 m., June 2, 1934, *St. John 14844* (type) (B); northwest slope Mt. Duff, in woods on low bushes, alt. 110 m., May 24, 1934, *St. John 14488*. (B).

Mangarevan name "*tara koa*" (acc. Theophile, a native informant).

This species seems to resemble most closely the widespread Indo-Malaysian *G. tiliaefolia* and *G. javanica* and also certain similar American species but differs from all in the dimorphic leaves and in the tuft of hair surrounding the styles. This whole group of species of *Gouania* badly needs revision. Perhaps all might be united into one large species with many varieties, as they closely resemble each other. However, certain details in the formation and hairiness of the disk, and especially in the length and degree of union of the styles seem significant. All specimens of *G. tiliaefolia* and *G. javanica* examined except one had very short styles. Most of them had more prominent bracts and less paniculate inflorescences than *G. mangarevica*. More distantly related are *G. vitifolia* of Hawaii, with shorter spikes and quite different leaves, and *G. Richii* of Fiji, with almost glabrous leaves and with the styles united part way up.

Hooker and Arnott (Bot. Beechey Voy. 61, 1832) report *Gouania dominguensis* L., an American species, from the Society Islands, citing a Lay and Collie collection, and many subsequent authors have credited the species to these islands, presumably on the basis of this report. To my knowledge no other collection has been cited. The authorities at Kew are unable to locate this Lay and Collie specimen, so its identity may not be determined. However, remembering that Hooker and Arnott regarded most of southeastern Polynesia as included in the Society Islands, and since no other *Gouania* has been found in southeastern Polynesia, I think it quite probable that the Lay and Collie specimen belonged to *G. mangarevica*. The expedition spent some time in Mangareva and is known to have collected several other plants there. It is unlikely that it was an American species, unless there was a confusion in labeling, as with several other plants collected by this expedition.

Fruiting specimens are much to be desired.

#### DIOSPYROS

While working up the Hawaiian species of *Diospyros* I found it neces-

sary to determine the status of the *Maba sandwicensis* reported by Seemann and subsequent authors from Fiji. This did not prove as easy to settle as was expected, and led to a considerable study of various Pacific Ebenaceae, and comparison with available Malaysian and Asiatic material. No attempt was made at a revision of the Pacific species of this group, but some observations were made which seem worth recording. The specimens studied are mainly in the herbaria of the New York Botanical Garden and the Bishop Museum, designated here respectively as (N) and (B). Dates of collections are not cited when collectors' numbers are available.

The recent study of the Malaysian Ebenaceae by R. C. Bakhuizen van den Brink (Bull. Jard. Bot. Buit. ser. 3, XV<sup>1</sup>, 1936; XV<sup>2</sup>, 1937) treats some of the Pacific species and makes the combinations for several of them under *Diospyros*, but touches upon the extra-Malaysian ones only incidentally. Bakhuizen's reasoning (Gard. Bull. Str. Sett. 7, pt. 2, 1933) in reducing *Maba* to *Diospyros* seems, in the light of these further studies of Pacific species, to be thoroughly sound, and necessitates the transfer of several Pacific island species from *Maba* to *Diospyros*. Other transfers are doubtless to be made, but material has not been available to determine their exact status.

*Diospyros* subgen. *Maba* sect. *Ferreola*

**Diospyros** L. subgen. **Maba** (Forst.) Bakh sect. **Ferreola** (Roxb.)

Fosberg, n. comb.

*Ferreola* Roxb. Pl. Corom. 1: 35, t. 45, 1795.

*Maba* sect. *Ferreola* Hiern, Trans. Cambr. Philos. Soc. 12: 108, 1873.

*Diospyros* subgen. *Maba* sect. *Forsteria* Bakh. Bull. Jard. Bot. Buit. ser. 3, XV<sup>2</sup>: 50, 1937.

Hiern's name *Ferreola*, based on Roxburgh's genus *Ferreola* (credited to Koenig by Index Kewensis), seems to be the earliest to have been used in the sectional category for this group of species, and so by the rule of priority must replace *Forsteria*. It may be argued that Hiern's section of *Maba* was more inclusive than Bakhuizen's section of *Diospyros*, but the type species of Roxburgh's genus was *Ferreola buxifolia* (*Diospyros ferrea*) which was also included in Hiern's section *Ferreola* and is the principal species of Bakhuizen's section *Forsteria*, though no type species was designated. This seems to make all three nomenclatorially equivalent, and therefore the earliest name must take precedence.

The present studies show that there are at least five distinct species belonging to this section, and a number of additional varieties in the two original species.

**Diospyros ferrea** (Willd.) Bakh., var. **nandarivatensis** (Gillespie) Fosberg, n. comb.

*Maba nandarivatensis* Gillespie, Bish. Mus. Bull. 74: 13, 1930.

Bakhuizen reduces this species outright to *D. ferrea* var. *sandwicensis*, but it seems to me to present differences enough to be maintained as a variety. The leaf-shape is not that of var. *sandwicensis* and the fruit is more nearly that of var. *littorea*. The branched inflorescence (in the staminate plant as shown by *Smith 544* as well as in the pistillate as described by Gillespie) suggests that it may have some relationship with *D. ellipticifolia*, and, indeed, except for the small size of the fruit, might equally well be placed in the latter. It certainly connects the two.

As recognized here, the size of the leaves and fruits varies considerably, but there seems no place to draw a line between them. Those with large leaves tend to have large fruits, but this is not constant.

*Specimens examined:*

FIJI Is.: Viti Levu, Tholo North Prov., Nandarivatu, *Gillespie 3764* (N); Vanua Levu, Thakaundrove, Natewa Peninsula, Uluingala, *Smith 1982* (N); Vanua Levu, Thakaundrove-Malhuata boundary, crest of Korotini Range, bet. Navitho Pass and Mt. Ndelaikoro, *Smith 544* (N); Vanua Levu, Mbua, southern portion of Seatovo Range, *Smith 1564* (N); Kandavu, hills above Namalata and Ngaloa bays, *Smith 126* (N).

CAROLINE Is.: Yap, *Kanehira 11840* (N).

PALAU Is.: small islands near Korrör, *Herre 29* and *36* (N).

The last four collections cited have much larger leaves than the first four.

**Diospyros ferrea** (Willd.) Bakh., var. **Gillespiei** Fosberg, n. var.

Ramuli glabrati; folia coriacea elliptica vel oblonga subsessilia canaliculata, nervis supra impressis; fructus subsessilis 1.5–2 cm. longus; calix in fructu glaber.

Branches and branchlets gray, beset with prominent lenticels, strigose when very young, but early glabrate; leaves stiff-coriaceous, elliptical to oblong, subsessile, canaliculate, the veins prominently impressed above, the blade up to 8 cm. long and 3.5 cm. wide, glossy, minutely appressed puberulent when very young, but soon becoming glabrate; flowers not seen; fruits subsessile, cylindric to ellipsoidal, sparsely appressed hirtellous, 1.5–2 cm. long, tipped with the persistent style; fruiting calyx cupulate, 7–8 mm. across, its lobes rounded to obtuse, low, glabrous inside, glabrous or almost so outside.

FIJI Is.: Viti Levu, Naitasiri Province, woods near road beyond Tamavia village,  $7\frac{1}{2}$  mi. from Suva, alt. 150 m., *Gillespie 2450* (B, N); same loc., *Gillespie 2146* (B), (type).

Referred by Gillespie to *Maba sandwicensis*, by A. C. Smith to *Maba buxifolia*, and by Bakhuizen to *Diospyros ferrea* var. *littorea*.

**Diospyros ferrea** (Willd.) Bakh., var. **subimpressa** Fosberg, n. var.

Ramuli glabrati; folia coriacea elliptica glabrata, nervis supra subimpressis; fructus ovoideus vel ovalis strigosus, calix in fructu planus vel reflexus strigosus.

Branches brownish, beset with prominent lenticels, sparsely strigose when young, glabrate; leaves stiffly coriaceous, elliptical, acute at base, rounded-acute at apex, sparsely strigose beneath when young, glabrate, the veins somewhat impressed above, the petiole about 2.5 mm. long; flowers not seen; fruits solitary on peduncles 2 mm. or less long, ovoid to broadly oval, up to 15 mm. long and 13 mm. wide, tipped with the persistent style, rather persistently strigose; fruiting calyx flat or with lobes reflexed, about 7 mm. wide, the lobes low, obtuse, strigose inside and outside.

FIJI Is.: Viti Levu, Rewa Province, woods near summit of Korom-bamba mountain, *Gillespie* 2324 (B), (type).

Very close to var. *Gillespiei*, differing chiefly in the shape of the fruit and in the less conspicuously impressed veins. Referred to *Maba sandwicensis* by Gillespie.

**Diospyros ferrea** (Willd.) Bakh., var. **savaiiensis** (Christ.) Fosberg, n. comb.

*Maba savaiiensis* Christophersen, Bish. Mus. Bull. 128: 173, 1935.

Characterized by coriaceous leaves, reticulate on both sides, abruptly contracted, then shortly attenuate into a petiole, blade ovate-acute, fruiting calyx reflexed, appressed puberulent inside and out, and fruit appressed puberulent. Plant otherwise glabrous or very early glabrate.

SAMOA: Savaii, Falealupo-Fagalele, *Christophersen* 3328 (N).

**Diospyros ferrea** (Willd.) Bakh., var. **angustifolia** (Miq.) Bakh.

*Schlechter* 19205 from "Walder bei Alexishafen, Kaiser-Wilhelmsland" (N) is, so far as I know, the first record of this variety from New Guinea. It agrees well with material of this variety (*Thwaites*; *DeSilva* 43 from Ceylon (N), cited by Bakhuizen. The other two specimens cited by him, *Stocks* from Malabar Concan (N) and *Kajewski* 932 from the New Hebrides (N) do not agree so well, and probably do not belong to this variety.

**Diospyros ellipticifolia** (Stokes) Bakh., var. **elliptica** (Forst.) Fosberg, n. comb.

*Maba elliptica* Forst. Char. Gen. Pl. 122, t. 61, 1776.

*Ferreola ellipticifolia* Stokes, Mat. Med. 535, 1812.

This, the typical form with elliptic obtuse leaves, dull and venulose above, may be reported, I think for the first time, from Niuaofou, (*Jaggar*, Oct. 1930, (B)).

This variety is widespread from Samoa to Malaysia and southeastern



Asia. Specimens were examined from Samoa, New Caledonia, and Amboina (all N). Forster's original material came from Tonga.

**Diospyros ellipticifolia** (Stokes) Bakh., var. *iridea* Fosberg, n. var.

*Maba* aff. *elliptica* Christophersen, Bish. Mus. Bull. 128: 173, 1935.

Arbor, ramuli aureo-sericei glabrati; folia lanceolata; flores paniculatae; fructus 23–25 mm. longus leviter umbonatus; calix in fructu cupulatus glabratus.

Tree 6 m. tall, branches terete, grayish brown, rather smooth; leaves not congested; young parts at first golden-sericeous, very early glabrate; leaves lanceolate, slightly acuminate, blunt, up to 11 cm. long and 3 cm. wide, chartaceous, glossy, drying an almost iridescent gray-brown, the petiole 3–5 mm. long; staminate flowers in loose 4–5 flowered panicles about 10–13 mm. long, panicle and calyx densely sericeous; calyx tube 2 mm. long, lobes 1 mm., acuminate; corolla tube cylindrical, 4 mm. long, 1 mm. wide, sericeous just beneath the lobes, otherwise glabrous, lobes ovate, 1 mm. long, sericeous; pistillate flowers not known; fruit on a peduncle 1 cm. long, red when ripe, yellow when immature, 23–25 mm. long, 15 mm. wide, slightly umbonate at apex; fruiting calyx glabrate, cupulate, 7–8 mm. across, lobes obtuse.

SAMOA: SAVAII, near Tufutafoe, alt. 10 m., *Christophersen* 2272 (B, N), 3310 (B, N) (type); (type sheet B). No. 2272 is in flower and no. 3310 in fruit.

Differs from var. *elliptica* in the shiny thin lanceolate leaves, light colored smooth twigs, acuminate calyx lobes, pedicellate flowers, much smaller calyx and corolla, and red fruit.

**Diospyros lateriflora** (Hiern) Bakh.

This species may be reported from Uvea on the basis of *Burrows* W. 23 "inland, edge of forest, el. 15 m." (B). Burrows gives the aboriginal name as *mapa*. This specimen was labeled *Maba sandwicensis* in the herbarium. *Parks*, 16291 from Liku Terrace, Eua, Tonga Is. (N) and a collection from Tonga, without island or locality, *McKern* 99 (B), also belong to this species.

Some doubt was expressed by Bakhuizen in assigning this species to his section *Forsteria*. The material at hand shows that the ovary is definitely 3-celled, the cells 2-ovuled, the ovary hairy, the style trifid, and staminodia absent; seeds were not available, so the endosperm could not be examined. There seems little doubt that it belongs in this section, here called *Ferreola*.

**Diospyros globosa** (A. C. Smith) Fosberg, n. comb.

*Maba globosa* A. C. Smith, Bish. Mus. Bull. 141: 121, 1936.

This is close to *D. lateriflora*, as Smith says. It may eventually prove only a variety, if further collecting should reveal intergrades, as the differences are no greater than the extremes in *D. ferrea* and *D. ellipticifolia*.

Material now available does not justify any change in its status, other than the generic transfer.

The fruits on *Smith 1242* are not mature and would probably approach in size those of *D. lateriflora* at maturity.

FIJI Is.: Kambara, *Smith 1241* (isotype), *1242* (both N).

**Diospyros Christophersenii** Fosberg, n. name

*Maba samoensis* Hiern, Jour. Bot. 15: 99, pl. 186, 1877.

Not *Diospyros samoensis* Gray.

Amplly characterized by Hiern. Known only in fruit. Probably to be placed in sect. *Ferreola*, though in absence of flowering specimens this is uncertain.

SAMOA: Savaii, Siuvao-Auala, *Christophersen 3379* (N).

*Diospyros* subg. *Maba* sect. *Cupulifera*

**Diospyros** L. subgen. **Maba** (Forst.) Bakh. sect. **Cupulifera** Fosberg, n. sect.

Calix in fructu insigniter accrescens, fructum usque ad medium cingens.

Fruiting calyx extremely accrescent, woody, surrounding the lower half of the fruit; ovary trilocular; fruit and calyx copiously rusty pubescent.

*Diospyros rufa*, characterized by its peculiar acorn-like fruit, was placed in *Maba* sect. *Ferreola* by Hiern, and would go, according to Bakhuizen's key, into sect. *Forsteria*, but seems to have little in common with the rest of the members of the section. Those who follow a narrow genus concept would doubtless refuse to include them in the same genus. So far as I know, the type species, *D. rufa*, in the sense accepted below, is the only species in the section described above.

**Diospyros rufa** (Labill.) Fosberg, n. comb.

*Maba rufa* Labill. Sert. Austr. Caled. 33, t. 36, 1824.

*Maba sericocarpa* F. Muell. Fragm. 5: 164, 1866.

*Maba cupulosa* F. Muell. Fragm. 5: 164, 1866.

*Diospyros sericocarpa* F. Muell. Austr. Veg. in Intercol. Exh. Ess. 1866-67: 35, 1867.

*Diospyros cupulosa* F. Muell. Austr. Veg. in Intercol. Exh. Ess. 1866-67: 35, 1867.

*Maba yaouhensis* Schlecht., Engl. Bot. Jahrb. 39: 226, 1906.

?*Maba parviflora* Schlecht., Engl. Bot. Jahrb. 39: 226, 1906.

Material of this species from New Caledonia has generally broader and more obtuse leaves than that from Australia.

Schlechter's species cannot, on the basis of material available, be maintained as specifically distinct. The small flowers of the material upon which *M. parviflora* was based suggest that if more material were available it might prove to be a good variety.

## RANDIA

***Randia cochinchinensis*** (Lour.) Merr. Tr. Am. Phil. Soc. 24 (2): 365, 1935.

*Aidia cochinchinensis* Lour. Fl. Cochinch. 143: 1790.

*Stylocoryne coffeoides* Gray, Proc. Am. Acad. 4: 309, 1860 (excl. syn.).

*Randia coffeoides* (Gray) B. & H. Gen. Pl. 2: 88, 1873.

*Randia Graeffei* Reineke, Engl. Bot. Jahrb. 25: 683, 1898.

Full synonymy in Merrill, Tr. Am. Phil. Soc. 24(2): 365, 1935.

The widespread Pacific *Randia coffeoides* does not seem to differ significantly from the above tropical Asiatic and Malaysian species. Plants from Polynesia and Micronesia tend to have the buds slightly bent and sharper at the apex than most Asiatic specimens, but some, even from Ceylon, cannot be distinguished from those from the Pacific. Neither can I distinguish *R. Graeffei* on the basis of the description and a number of collections from Samoa. I have not seen the type. It is considered by Kanehira (Bot. Mag. Tokyo 45: 349, 1931) to be a synonym of *R. racemosa* (Cav.) F.-Vill., itself a synonym of *R. cochinchinensis*.

*Stylocoryne coffeoides* Gray was so inadequately characterized that it is doubtful whether it could be considered validly published. Neither specimens nor localities were cited, and both synonyms given by Gray have been shown by Seemann (Fl. Vit. 123) to belong to other genera altogether. The U. S. Exploring Expedition specimens and a collection by Harvey labeled by Gray are the only means of positive identification of the species. Duplicates of these that I have seen in the herbarium of the New York Botanical Garden are certainly *R. cochinchinensis*. Seemann (l.c.) considered these identical with *Stylocoryne racemosa* Cav. which Gray definitely excluded from his species. Merrill (l.c.) considers *S. racemosa* Cav., of the Philippines, to be a synonym of *R. cochinchinensis*. This seems to add the weight of Seemann's opinion to my reduction of *R. coffeoides* to *R. cochinchinensis*.

The range of the species in the Pacific extends from the Society Islands westward through most of the major island groups to Malaysia, and beyond through tropical Asia. It has been collected from most of the high island groups including the Societies, Samoa, Wallis, Fiji, Tonga, New Hebrides, Solomons, Marianas, Carolines, Palau, etc. It does not occur in the Hawaiian Islands, and has not been collected in the Cook Islands or the Marquesas, and, strangely enough, apparently not in New Caledonia. It may here be reported from the island of Niuafoou on the basis of a specimen in the Bishop Museum collected by T. Jagger, Oct. 1930.

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## Studies on Rhizophidium

### II. Rhizophidium laterale

J. S. KARLING  
(WITH PLATE 31)

*Rhizophidium laterale* (Braun) Rabenk. is one of the earliest known chytrid species which was first described and figured by Braun (1855) on healthy and dead cells of *Ulothrix zonata* in Germany. He placed it in the subgenus *Phylyctidium* because of its unbranched knob and peg-like haustorial or absorbing system, and most investigators since that time have retained it in this group. In 1868, however, Rabenhorst transferred it to Schenk's (1858b) new genus *Rhizophidium*, where it was retained by Fischer (1892). It has subsequently been reported to occur on *U. zonata* and *Mougeotia* sp. in Germany (Schenk, 1858a, 1858b), *Stigeoclonium* sp., and *U. zonata* in Russia (Sorokin, 1883, 1889; Serbinow, 1907), and *Spirogyra* sp., in New York, U. S. A. (Sparrow, 1932). During the early summer of 1938 I found it in great abundance on *U. zonata* in Candlewood Lake, Connecticut, and my studies have brought to light certain structural characters and other data which necessitate the transfer of this species to *Rhizophidium*, as this genus is now recognized, and cast considerable doubt on the claim that it is ubiquitous as to host range.

#### HOST RANGE

Shortly after this chytrid had been brought into the laboratory, experiments were begun to determine its host range. These tests involved killed as well as living cells of *Hydrodictyon reticulatum*, *Spirogyra crassa*, *Spirogyra* sp., *Stigeoclonium tenue*, *Draparnaldia* sp., *Nitella flexilis*, *Chara coronata*, pollen grains of *Pinus austriaca* var. *nigra*, *P. sylvestris*, *P. densiflora*, *P. banksiana*, *P. Thunbergii*, and hemlock, ova of *Fasciola hepatica* and root tips of *Allium cepa*. The living cells and tissues were carefully examined and washed several times in sterile charcoal water, while the dead ones were transferred directly from the boiling water and dry heat oven in which they had been killed. These were then added to Petri dishes containing heavily infected filaments of *U. zonata*, placed in a cool place in front of an east window, and examined daily. As a check on whether or not these laboratory conditions were favorable and conducive to infection living and dead filaments of the algae listed above as well as onion root tips were tied up in small gauze bags and staked out in Candlewood Lake where the infected *Ulothrix* was growing.

The results of these laboratory and outdoor experiments were all negative. No infection of either the living or dead hosts has been observed

up to the present time. It is to be further noted that *Stigeoclonium tenue*, *Oedogonium* sp., *Cladophora glomerata*, and *Spirogyra* sp. were growing together with the infected *Ulothrix* in Candlewood Lake, and these were likewise free of infection. While these results and observations are somewhat limited and do not entirely preclude the possibility that *R. laterale* may occasionally infect other algae, they none the less suggest very strongly that it is limited to one host species.

The effect of *R. laterale* on the host cell is not always very marked, and it is often difficult to determine the degree of pathogenicity. Infected cells have been found whose protoplasm did not appear to be affected at all (fig. 1f), while others seemed to be distinctly injured. In the latter cases the chloroplasts gradually turn yellowish brown and begin to degenerate and eventually appear clumped with the starch grains, other granules, and the remainder of the protoplasm around the delicate rhizoidal strands, as is shown in figure 1a and 1b. In a few instances zoospores have been found germinating on dead cells and developing into mature thalli, which indicates that this chytrid may also be saprophytic. This is further borne out by my limited success in infecting killed *Ulothrix* filaments, as will be noted later.

#### STRUCTURE OF THE THALLUS

The development of this species has been briefly but well treated by Braun, and I shall confine my description largely to certain structural characters and developmental phases which have not yet been emphasized. *Rhizophidium laterale* is frequently gregarious, as is shown in figure 1, and in very exceptional cases as many as twelve thalli have been found on a single cell. A heavily infected filament of *Ulothrix* may accordingly have over a hundred sporangia irregularly distributed along its length. The mature sporangia may be spherical, slightly flattened, and oval, with one to three exit papillae. The spherical ones vary from 9 to 18 $\mu$  in diameter, with 13.5 $\mu$  as the average of a hundred sporangia measured at random. Of these sporangia 72 per cent were somewhat anatrope, with the exit papillae sublateral or near the base, 20 per cent had subapical or lateral papillae, and in 8 per cent the papillae were apical. In some thalli the exit papillae may be so near the base that they rest on the surface of the host cell. They may be comparatively low and inconspicuous or protrude 3–4 $\mu$  beyond the surface of the sporangium. Usually only a single papilla is present, but occasionally two and rarely three may be found. After deliquescence of the papillae the orifices may vary from 3–5 $\mu$  in diameter.

The wall of the sporangium likewise varies considerably in thickness. In some sporangia it is very thin, while in others it may be .8–1.7 $\mu$  in



breadth. Sporangia with such walls do not usually become wrinkled and collapse shortly after the zoospores have emerged. Sometimes an unexpanded portion of the zoospore or semispherical protrusion may be found near the base of the sporangium, as is shown in figures 1g, 1h, and 13, and such sporangia often appear very similar to *Chytridium Schenkii*, *C. gibbosum*, and *C. aggregatum*. These zoospore-case appendages may sometimes become thick walled and darken in color with age.

The most conspicuous feature of the absorbing system of this species is the knob and peg-like structure beneath the sporangium. For the sake of convenience I am calling this structure an haustorium, although as will become evident below, it is apparently not the primary means of food absorption. With the view of emphasizing this structure, I have drawn in figures 2 to 6 some of the variations which it may exhibit in various thalli. As Braun, Serbinow, and Sparrow have already shown, it may be short and tapering, almost filamentous, or inflated at the end to form a small globular apophysis-like structure which may become  $4\mu$  in diameter. In length it may vary from 4 to  $12\mu$ , and be even (figs. 2, 10, 11) or somewhat irregular in contour (figs. 4, 5, 6). It is usually very narrow in diameter and constricted a short distance below the base of the sporangium (figs. 2, 14), and in very rare instances it may become needle-shaped and run out to a fine point (fig. 15). It may terminate within the layers of the host wall, extend to the latter's inner boundary, or penetrate it completely into the cytoplasm of the cell. Oftentimes the inner boundary of the wall may be pushed in or swollen at the region where the haustorium comes into contact with it, as is shown in my figures 2 and 12, and Braun's figures 23 to 25. An interesting variation is shown in figure 3 in which the haustorium or peg has both an extra- and an intramatrical swelling similar to those of *Physorhizophidium pachydermum* (Scherffel, 1926; pl. 9, figs. 28, 33, 34). Figure 4 shows an irregular haustorium which extends through the wall and invaginates the plasma membrane. When thalli occur at the junction of two cells, the haustorium may extend down into the cross wall for a considerable distance before bending over and entering the lumen of the cell (figs. 1d, 1g, and 5). In figure 6 is shown a rare case in which the peg is comparatively slender, extends into the center of the cell and branches dichotomously.

The most important discovery in this study, however, is the presence of extremely fine, delicate thread-like branched rhizoids at the tip of the haustorium, which have heretofore been overlooked by previous workers. These rhizoids are so fine and delicate that very high magnifications and a special treatment of the host cells are necessary to render them visible. They have the appearance of delicate, hyaline cytoplasmic strands, and

are usually completely obscured by the host protoplasm. In living preparations they are never as sharply defined and distinct as I have drawn them but for the sake of emphasis I have purposely intensified their appearance. They were first detected in empty dead cells which had become infected, and at diameters of 2800 to 3400 I have been able to see them clearly in a number of instances. As a check on these observations, host cells were specially treated before infection to render them more transparent. Filaments of *Ulothrix* were immersed in potassium hydroxide for half an hour,

#### Explanation of Plate 31

Fig. 1. Five heavily infected cells of *Ulothrix zonata* showing sporangia in various stages of development.

Fig. 2-6. Variations in the haustorium, five rhizoids and their relation to the host cell wall and protoplasm. Fig. 2. Wall slightly pushed in at the tip of the haustorium, rhizoids branched and unusually extensive. Fig. 3. Haustorium with an extra- and intramatrix swelling. Fig. 4. Haustorium extending through the wall and invaginating the plasma membrane. Fig. 5. An elongated haustorium subtended by numerous fine rhizoids. Fig. 6. A branched haustorium which extends to the center of the host cell.

Fig. 7. Zoospores of *Rhizophidium laterale*.

Fig. 8. Germination of a zoospore on the host cell.

Fig. 9. Germination of a zoospore in water.

Fig. 10. An early stage in the development of a sporangium. Protoplasm vacuolate with several conspicuous refractive globules.

Fig. 11. A later stage showing the large central vacuole containing an unusually large globule. Exit papilla apical.

Fig. 12. A more mature anatrochous sporangium with non-vacuolate granular greyish protoplasm and a large refractive globule.

Fig. 13. A later developmental stage of a sporangium with two exit papillae and the unexpanded portion of the zoospore case. The protoplasm includes numerous small refractive globules more or less regularly spaced.

Fig. 14. An early stage in the emission of the zoospores.

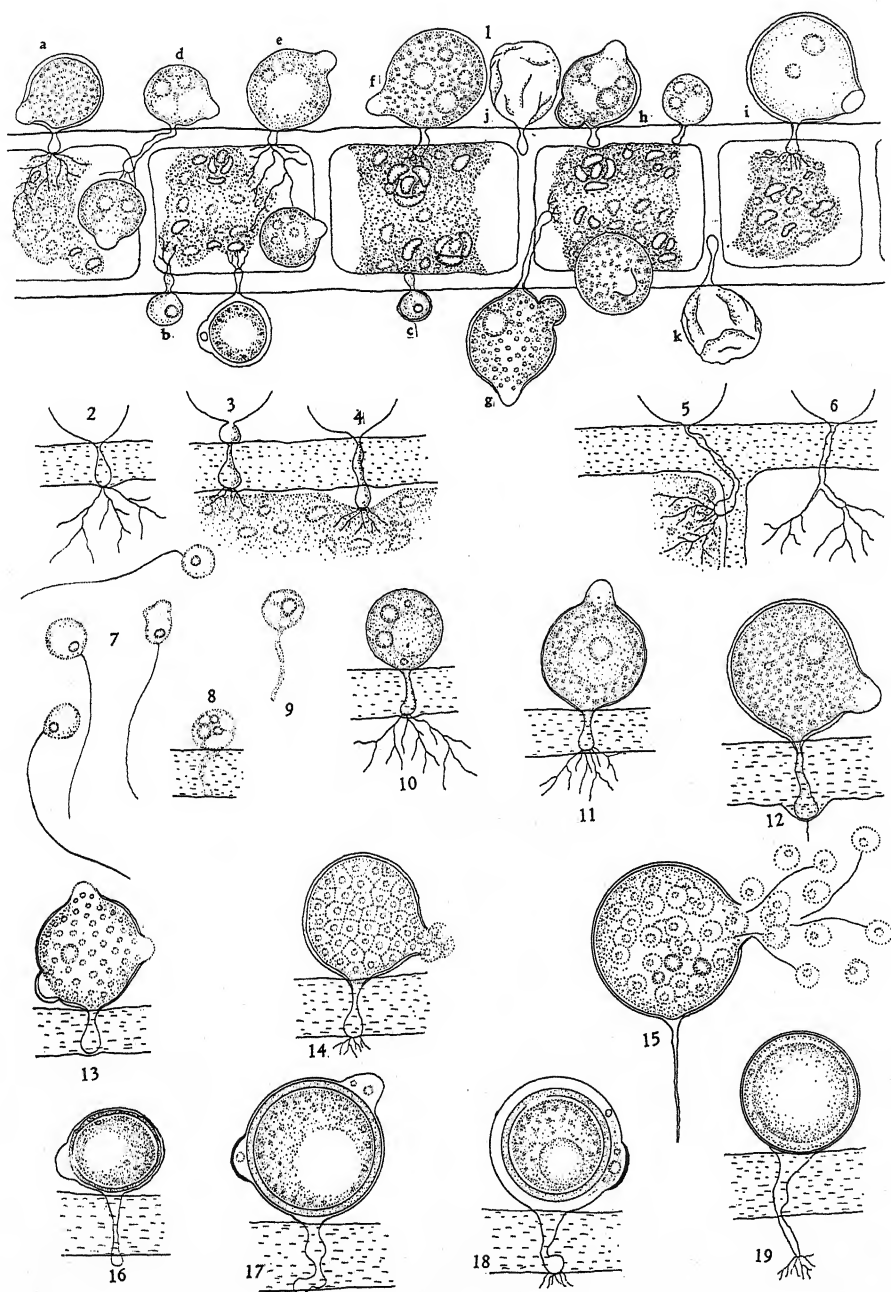
Fig. 15. A later stage after most of the swarmspores have emerged. Two large refractive globules are still present among the zoospores.

Fig. 16. A small oval resting spore with a lateral protrusion in the thin outer wall. Content appears as if it had contracted and encysted with a thicker inner wall.

Fig. 17. A large spherical resting spore with a lateral unexpanded portion of the zoospore case, and the subapical exit papilla of the incipient sporangium from which the spore developed. Inner wall thick yellowish amber and close to the thin outer one, spore content granular with a large vacuole.

Fig. 18. Another resting spore with the thick inner wall considerably removed from the thin outer one, suggesting again that in the incipient stage the contents contracted and encysted. A large refractive globule lies within the spore.

Fig. 19. Another spore in which the differentiation of an inner and outer wall is not distinct. The greater portion of the spore is occupied by a central refractive globule.



rinsed in water, and finally bleached overnight in hydrogen peroxide, which made the cell content optically homogeneous, pale yellowish green, and comparatively transparent. These filaments were then added to normal heavily infected cultures, and after a week a very few infections occurred. With careful examination at the magnifications noted above, the rhizoids of these thalli could be seen rather clearly. They may be branched and extend for a linear distance of  $12\mu$  (figs. 1a, 1d, 2, 5, 10, 11) or reduced, short, and brushlike (fig. 3, 4, 18, 19). In several cases only a single short filament has been seen, as is shown in figure 12, while in other instances I have been unable to see them at all.

As has been noted before, these delicate rhizoids at the tip of the haustorium have been overlooked by previous workers, and their presence makes it necessary to transfer this chytrid to the genus *Rhizophidium* if we are to maintain and recognize the present generic distinctions between it and *Phlyctidium*. While I do not believe, in our present state of knowledge concerning the rhizidiaceous chytrids, that these distinctions are of fundamental diagnostic value, I am none the less following Rabenhorst's disposition of this species for the time being.

#### DEVELOPMENT OF THE SPORANGIA

The zoospores of *Rhizophidium laterale* are hyaline and almost spherical  $2.5\text{--}3.2\mu$ , with a very small clear refractive globule situated toward the posterior end and a  $12\text{--}15\mu$  long cilium (fig. 7). My observations as to their shape differ thus slightly from those of Braun and Serbinow who describe and figure them as being oval and tapering at the posterior end. I have also observed some of this shape as they are emerging from the sporangia, but after they have been swimming about for some time, they become almost spherical. After coming to rest, the zoospores may undergo slight amoeboid changes in shape and movement, but these never become pronounced. The swarmspores which do not degenerate and come to rest on the host cell soon form a germ tube which penetrates the wall (fig. 8). Germination in water may also occur (fig. 9), but such swarmspores soon degenerate. In the process of germination the refractive globule remains in the spore and soon enlarges in size, and very frequently others appear shortly thereafter (fig. 8). In the meantime the remainder of the cytoplasm usually becomes highly vacuolate. Zoospores may occasionally encyst on the host and develop a comparatively thick wall before or shortly after the germ tube has been formed (fig. 1c), and in subsequent development the incipient sporangium apparently grows out as a vesicle on one side in the same manner as I have described (1938) for *Chytridium aggregatum*. Although I have not observed their development, I believe this

is the manner in which sporangia with zoospore case appendages (figs. 1g, 1h, and 13) arise.

The germ tube increases in diameter and usually enlarges at the tip to become the variously shaped haustorium described above. I have been unable to determine at what stage the delicate rhizoids appear, but I am of the opinion that they grow out from the germ tube after it has become well established as the haustorium. I have not so far observed any extensive branching of the germ tube to form the rhizoidal system as in *Diplophlyctis*, *Endochytrium*, *Entophlyctis*, etc.

In the early developmental stages the incipient sporangia usually possess a large central vacuole and one to several conspicuous refractive globules (fig. 10). The vacuole may persist for a long time, and in some instances include the refringent globules (fig. 11). It gradually disappears as the sporangium matures and the exit papilla are formed. By this time the protoplasm begins to lose its refractive appearance and becomes more greyish granular (fig. 12). After several hours, however, minuted refringent globules again appear in the cytoplasm (fig. 13), and the greyish granular appearance becomes less intense. The small refractive bodies are later included individually in the zoospore initials. It is to be particularly noted in figures 1f, 1g, 12, and 13 that one or more large globules are still present in the cytoplasm, and according to my observations, they do not break up to become included in those minuter bodies which go into the zoospores. In several sporangia in which they were found they persisted throughout the maturation stages, cleavage, and the emergence of the zoospores. While the swarmspores are swarming in the sporangium (fig. 15), they are continually spun and tossed about as extraneous bodies. They may occasionally be found in empty zoosporangia long after all zoospores have emerged (fig. 1i). The occasional presence and persistence of such bodies in the sporangia is unusual for species of *Rhizophidium* and constitutes the only outstanding aberration I have noted in the development of *R. laterale*.

In living material the zoospore initials become visible a few hours after the small refractive globules (fig. 13) appear. Swarmspore emergence has been observed but a few times, and I am thus unable to describe the range of variations in the process. The tip of the exit tube gradually deliquesces and a few of the zoospores begin to ooze out through the orifice to form a small globular mass (fig. 14). After a short pause they slowly pull apart and dash away. They do not appear to be imbedded in a large conspicuous globule of hyaline matrix, as in *R. sphaerocarpum*. After the initial spores have emerged, the remaining ones escape singly, in two's or three's, and, when approximately half of them have passed out, those within the sporangium begin to swarm very actively (fig. 15).



The empty thin-walled sporangia usually collapse partly and become wrinkled after the zoospores have emerged (fig. 1j, 1k), but the thick-walled ones retain their shape for a long time (fig. 1i). Numerous tests with chloro-iodide of zinc have been made on thalli and resting spores in various stages of development, but so far no cellulose reaction has been observed. With such treatment the walls turn yellowish and amber brown.

#### RESTING SPORES

The resting spores of *R. laterale* were found in abundance as the evanescent zoosporangia began to disappear in the latter part of June. They are smooth, oval, slightly oblong and spherical, 8–15 $\mu$  in diameter, hyaline, and yellowish to amber in color at maturity. Serbinow describes them as being hyaline, but I have often found that they may become distinctly amber in color as they grow old. Up to a certain stage they develop in the same manner as the evanescent sporangia, and no sexuality has so far been observed in relation to their formation. In a great number which I have studied the contents of the developing spore appear to have contracted in varying degrees, encysted, and become enveloped by a thick wall (figs. 16, 17, 18). In such cases it is possible to differentiate a comparatively thin hyaline outer wall which looks like an envelope around the spore (fig. 18). The yellowish and amber tint described above seems to be confined to the inner wall. In other instances the inner wall lies very close to the outer one (fig. 17), while in some spores (fig. 19) it is impossible to differentiate between the two. In many of the spores the outer wall has a disc-shaped or semi-spherical protrusion (figs. 16–18) which may often be recognized as a portion of the zoospore case. Occasionally refractive bodies and other small granules may be found between the inner and outer walls (figs. 17, 18).

Unlike most of the other species of *Rhizophidium*, the resting spores of this chytrid usually lack a large central refringent globule. According to my observations the content of the majority of spores is evenly granular with a fairly large central or excentric vacuole (figs. 16, 17). Sometimes, however, spores with globules (figs. 18, 19) may be found, but these appear to be comparatively rare. Figure 17 shows an interesting resting spore with the remains of an exit papilla on the outer wall. In its incipient stages this spore apparently reached the exit-papilla stage of sporangial development, and then its content was transformed into a resting spore. So far fermentation of the resting spore has not been observed.

#### DISCUSSION

As has been noted before, Schenk, Sorokin, and Sparrow reported this

species to occur on *Mongeotia* sp., *Stigeoclonium* sp., and *Spirogyra* sp., in Germany, Russia, and America, but in my cross inoculation experiments involving these hosts I have found no evidence to support their claim. Since these workers found only a few sporangia with lateral exit papillae, no resting spores, and made no cross inoculations with *Ulothrix zonata*, it is difficult to determine whether or not they were dealing with the same species. It is not improbable that several similar species with lateral exit papillae may exist, and until intensive developmental studies of the individual species as well as extensive cross inoculations have been made, we cannot be sure of their exact identity.

Sparrow is further of the opinion that the chytrid which Coker (1923) describes as *R. carpophilum* on oogonia of *Achlya apiculata* is identical with *R. laterale* but, except for the fact that Coker failed to figure a branched rhizoidal system, Sparrow has no basis for his claim.

Fischer, Serbinow, and Minden (1911) regard *Phlyctidium Haynaldii*, described by Schaarschmidt (1883) on *U. zonata* in Hungary, as identical with *Rhizophyidium laterale*, but this viewpoint is obviously open to question. Most of the sporangia figured by Schaarschmidt are strikingly different in shape and appearance with one or two conspicuous diverging apical papillae which make them broad at the apex and somewhat triangular in outline. Furthermore, the haustorial knob or peg is absent in most cases, and the absorbing systems consist primarily of an elongated, tapering filament.

In marine plant and animal remnants of Andree's polar expedition Lagerheim (1899) found empty sporangia of a chytrid on *Hormiscia implexa* from Greenland which he believes may relate to *P. Haynaldii*. The empty sporangia, however, are rounder than those described by Schaarschmidt, but since Lagerheim does not further describe or figure them, it is impossible at present to determine their identity.

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Studies in the Uredinales,  
the genus *Chaconia*<sup>1</sup>

E. B. MAINS

(WITH SIX FIGURES)

The genus *Chaconia* was described by Juel (5) in 1897, the type species being *C. alutacea* based on a collection made by C. A. M. Lindman, July 15, 1893, near Asuncion, Gran Chaco, Paraguay. The host was given as *Calliandra*, later determined as *Pithecolobium divaricatum* (Borg.) Benth. It was distributed by Vestergren (Microm. rar. sel. 755). Only telia were described. *Chaconia* was known only from the type collection until 1935, when the writer (6) discovered it on a phanerogamic specimen in the Herbarium of the University of Michigan. The specimen was collected by W. A. Shipp (no. 621A) from the Sittee River, British Honduras, Sept. 4, 1930 (figs. 1-2). The host was doubtfully reported as *Pithecolobium Peckii*. It apparently is *P. Recordii*. In addition to telia, pycnia and a few old uredinia were found on this collection.

Juel considered that the species was unusual and not closely related to any rust known at that time. He described and illustrated the teliospores as one-celled, with hyaline, thin walls. He states that they occur in groups of 4 or occasionally 5 or 6 on basal cells and that they are produced in succession, the younger pushing the older to one side as they develop. The teliospores of the collection from British Honduras agree very well with those of the type collection and Juel's description. The pycnia of this collection are subcuticular and the urediniospores are echinulate.

Another collection of this species was discovered in the course of a study of species of *Maravalia*.<sup>2</sup> This is a collection on *Pithecolobium glomeratum* collected by E. Ule (no. 3500) at Seringal, Auristella, Rio Acre, Peru, July 1911. The Sydows (7) based their species *Uromyces pallescens* on this collection and later it was transferred to *Maravalia* (Dietel, 3). This collection has sessile, hyaline teliospores in groups of 2-4 on basal cells (fig. 3). It is evident that this also is *Chaconia alutacea*.

The Sydows (8) have described a species of *Blastospora*, *B. Bulleri* based on a collection of *Jasminum malabaricum* collected by S. L. Ajrekar

<sup>1</sup> Papers from the Department of Botany and Herbarium of the University of Michigan. This study developed out of an investigation of tropical American Uredinales supported from the funds of the Horace H. Rackham School of Graduate Studies.

<sup>2</sup> The writer is indebted to Dr. G. B. Cummins for the loan of collections from the Arthur Herbarium of Purdue University and to Professor G. Samuelsson for collections from the Naturhistoriska Riksmuseet, Sweden.

at Matheran, Bombay, Nov. 15, 1911 (E. J. Butler no. 1603). The teliospores are described as one-celled, clavate-cylindric or fusoid, hyaline, short pedicellate and fasciculate at the base. A study of Sydow Fungi exot. 329 shows that the teliospores develop in groups of 5-9 from the upper portion of a basal cell and are sessile (fig. 4). *Blastospora* was described by Dietel (2) and based on *B. smilacis* which has globoid teliospores with well developed pedicels. *Blastospora Butleri* should therefore be transferred to *Chaconia*.

Arthur (1) has doubtfully described a species in *Chaconia* under the name *Chaconia* (?) *texensis*. This was based on a collection on *Phoradendron macrophyllum* (Engelm.) Cockerell, obtained by W. H. Long (947) at Austin, Texas, May 8, 1901. This specimen has been available for study. The fungus develops a pulvinate, pseudoparenchymatous mass, apparently beneath the cuticle. Imbedded in this are one- and two-celled hyaline spores. The manner in which these spores develop is uncertain but it is evident that they are not grouped on basal cells and this is not a species of *Chaconia*. It is not certain whether this is a rust.

*Chaconia* has been variously placed in the classifications of the Uredinales. The Sydows (9) have placed it in the Melampsoraceae because they considered that the basal cells were more or less united in a layer. They were uncertain concerning its position in the family.

The basal cells are generative cells. As Juel has pointed out the teliospores bud out from them in succession. The oldest often germinates before the youngest reaches full development (fig. 3). The teliospores are therefore sessile. This sessile character has been considered one of the principal diagnostic characters of the Melampsoraceae. However, the teliospores are not united laterally and do not form compact crusts as in the Melampsoraceae. Apparently *Chaconia* represents a transition from the Melampsoraceae to the Pucciniaceae.

The successive development of a number of teliospores from a basal cell is not unusual in the rusts. In most species however, the basal cells form a compact layer and the lateral budding is not easily demonstrated. In *Chaconia*, the basal cells are laterally free and tear away from the rest of the mycelium in making mounts for the microscope, carrying their teliospores with them.

Several species of *Maravalia*, a genus in the Pucciniaceae with well developed pedicels, have their teliospores grouped on free basal cells. Therefore, *Chaconia* is apparently more closely related to genera in the Pucciniaceae than to any genus which has been included in the Melampsoraceae.

Arthur (1) has included *Chaconia* in the Aecidiaceae (Pucciniaceae)



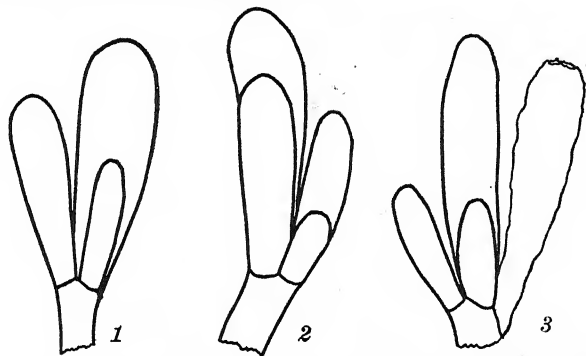
in the subfamily Skierkatae with *Skierka*, *Ctenoderma* and *Sphenospora*. It does not show any close relationship to these genera which have a very different development of their teliospores.

Dietel (4) has placed *Chaconia* in the Pucciniaceae in the tribe Oliveae with *Calidion*, *Olivea*, *Chrysocelis*, and *Goplana*. This appears to be a logical position for it. The teliospores of *Olivea* develop in a very similar manner.

CHACONIA Juel, Bihang K. Svenska Vet.—Akad. Handl. 23: 12. 1897.

Pycnia subcuticular. Uredinia subepidermal, pulverulent; urediniospores obovoid to ellipsoid, echinulate or finely verrucose in irregular lines. Telia subepidermal, soon naked; teliospores clavate to cylindric, hyaline, thin-walled, sessile arising in succession from basal cells, a number from a basal cell, the basal cells free laterally, germinating immediately.

Type species *Chaconia alutacea* Juel.



Figs. 1-3. *Chaconia alutacea*. 1 and 2, groups of teliospores from Shipp's collection no. 621A; 3, group of teliospores from the type of *Uromyces albescens*; the spores are in various stages of development, one having germinated in fig. 3.  $\times 600$ .

CHACONIA ALUTACEA Juel, Bihang K. Svenska Vet.—Akad. Handl. 23: 12. 1897.

*Uromyces albescens* Syd. Ann. Mycol. 14: 66. 1916.

*Maravalia albescens* Syd. in Dietel. Ann. Mycol. 22: 270. 1924.

Pycnia amphigenous, subcuticular, lenticular,  $20-24 \times 60-70\mu$ .

Uredinia hypophyllous, subepidermal, grouped in somewhat hypertrophied tissue opposite the pycnia, 0.5-1 mm. in diameter; urediniospores ellipsoid,  $16-20 \times 22-26\mu$ , the wall cinnamon-brown,  $2\mu$  thick, moderately echinulate, the pores obscure.

Telia hypophyllous, subepidermal, small, scattered or in small groups; teliospores clavate or cylindric,  $10-18 \times 40-70\mu$ , the wall hyaline, very thin,  $0.5\mu$ , sessile, 2-4 sometimes 5-8 arising in succession from a basal cell, germinating at once (figs. 1-3).

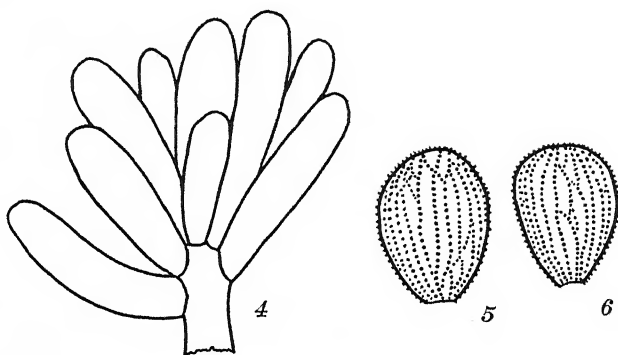
## Specimens examined:

*Pithecolobium divaricatum* (Borg.) Benth. Asuncion, Gran Chaco, Paraguay, July 15, 1893, C. A. M. Lindman (Vestergren, Microm. rar. sel. 755) type.

*Pithecolobium glomeratum* Benth. Serigal, Auristella, Rio Acre, Peru, July 1911, E. Ule (3500).

*Pithecolobium Recordii* Standl. Sittee River, British Honduras, Sept. 4, 1930, W. A. Shipp (621A).

Juel (5, pl. 3, fig. 15) shows a basal cell which is branched with four spores on each branch. In the specimens examined only simple basal cells have been noted with a maximum of 6 spores.



Figs. 4-6. *Chaconia Butleri*. 4, group of teliospores; 5 and 6, urediniospores, surface view to show markings.  $\times 600$ .

*CHACONIA BUTLERI* (Syd.) nov. comb.

*Blastospora Butleri* Syd. Ann. Mycol. 10: 266. 1912.

Uredinia hypophyllous, subepidermal, on discolored spots up to 1 cm. across, more or less circinating, pale yellow, pulverulent; urediniospores obovoid or ellipsoid,  $18-24 \times 26-34\mu$ , the wall hyaline,  $2-3\mu$  thick, finely verrucose in irregular longitudinal lines which somewhat anastomose, the pores obscure (figs. 5-6).

Telia hypophyllous, subepidermal, associated with the uredinia, pale brown, pulvinate, waxy; teliospores cylindric or clavate,  $9-12 \times 44-54\mu$ , the wall hyaline, very thin,  $0.5\mu$ , sessile, 5-9 arising in succession from a basal cell, germinating immediately (fig. 4).

## Specimen examined:

*Jasminum malabaricum* Wright, Matheran, Bombay, India, Nov. 5, 1912, S. L. Ajrekar (Syd. Fungi exot. exsicc. 329).

The urediniospores of this collection are pedicellate. The verrucose

markings in lines give a beaded appearance to the spores. The teliospores occur in various stages of development in definite clumps on basal cells.

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## The cytology of *Cuscuta*

SIDNEY O. FOGELBERG

(WITH PLATE 32)

### INTRODUCTION

Investigations of the physiology, morphology and taxonomy of various species and groups of species within this large genus (about 159 species) have been numerous. (For bibliography see Yuncker, 1920, and Dean, 1937.) The most extensive treatment of the genus to date is the monograph by Yuncker (1932), and the present paper follows his nomenclature. Where synonyms have been used by workers cited, Yuncker's accepted name is given in parentheses.

Fedortschuk (1931) observed the haploid number of chromosomes of *C. epithymum* Murr. to be 7. His lateral views of the division of the microspore nucleus seem to be the only published figures of equatorial-plate chromosomes in any species of *Cuscuta*.

Finn and Safijovska (1934), investigating microgametophyte-development and the numbers and forms of the chromosomes in divisions of somatic as well as of "haploid" nuclei (presumably in the pollen grain) report the following numbers:

<i>C. epithymum</i> Murr. var. <i>vulgaris</i> Engelm. ( <i>C. epithymum</i> Murray)	$n = 7$	$2n = 14$
<i>C. europaea</i> L.	$n = 7$	$2n = 14$
<i>C. epilinum</i> Weihe	$n = 21$	$2n = 42$
<i>C. arvensis</i> Beyr. var. <i>calycina</i> Engelm. ( <i>C. campestris</i> Yuncker)	$n = 28$	$2n = 56$

As these authors point out, this is evidently a polyploid series with the basic number 7. Two of the three subgenera into which the genus is divided are represented. They find further evidence as to the basic number in the fact that one large chromosome for each set of 7 is present in both haploid and diploid nuclei in all four species.

According to Yuncker, *C. epilinum*, *C. epithymum*, and *C. europaea* belong to the subgenus CUSCUTA. *C. campestris* is included in the subgenus GRAMMICA. The only representative of the subgenus MONOGYNA which Finn and Safijovska examined was *C. monogyna* Vahl. Although the chromosome number was not determined, it differs from the others studied in having much larger chromosomes. It was found to be unique, too, in certain details of development of the microgametophyte, so that there apparently exists here an observable correlation between the cytological details and the previously observed morphological characters upon which taxonomists have based the major divisions of the genus. However, the authors point out that any statement in regard to evidence of inter-



relationships from cytological observations must carry little weight until a larger number of species has been investigated.

#### MATERIALS AND METHODS

Seeds of *Cuscuta* species were obtained from collections of mature capsules and from specimens in the herbaria of the following institutions: Missouri Botanical Garden, the University of Michigan, the University of Wisconsin, and the Gray Herbarium. The species studied and the places of collection of the plants producing seeds are as follows:

- C. Gronovii* Willdenow, Madison, Wis.
- C. Cephalanthi* Engelm., Madison, Wis.
- C. glomerata* Choisy, Port Byron, Ill.
- C. compacta* Jussieu, Langely, Ark.
- C. pentagona* Yuncker, Greencastle, Ind.
- C. campestris* Yuncker, Quitman, Ark.
- C. Coryli* Engelm., Wonewoc, Wis.
- C. indecora* var. *neuropetala*, (Engelm.) Hitchcock, Ashley, N.D.

The seeds were germinated in moist chambers after the seed coats had been nicked or scarified. When the seedlings were about 2 cm. long they were placed on stems or petioles of a host plant under a bell jar. When one of the seedlings had formed prehaustoria the bell jar and the remaining seedlings were removed. The host plants were chosen to some extent from the lists given by Yuncker (1932) and Dean (1934, 1935); but for the most part a number of available greenhouse plants were tried and those which appeared most favorable were retained.

Most of the cytological work was done on flower buds, but a few stem tips and stems with incipient haustoria were used for study of the somatic divisions. A variety of fixatives and stains were used with all species, but for all but *C. pentagona*, *C. campestris*, and *C. compacta* fixation in Belling's modification of Navashin's fluid followed by the crystal violet-iodine stain proved most satisfactory, especially for the study of chromosomes at or near the equatorial-plate stage. *C. pentagona* and *C. campestris*, although appearing to be satisfactorily fixed in both Belling's and Randolph's modifications of Navashin's fluid when stained in Heidenhain's iron-alum haematoxylin, could not be induced to take a satisfactory crystal-violet stain. *C. compacta* was most satisfactorily fixed in Flemming's strong solution.

The material was imbedded in paraffin and sectioned at thicknesses of 5-12 $\mu$  for the study of equatorial-plate chromosomes and of 18-30 $\mu$  for the study of diakinesis and other prophase stages.

A few preparations were made using the aceto-carmin smear technique

and a few according to Taylor's smear method, but the minuteness of the anthers made both these procedures unsatisfactory.

#### OBSERVATIONS

Examinations of longitudinal and transverse sections of the developing primary roots of seedlings of *C. Gronovii*, *C. Cephalanthi*, *C. Coryli*, *C. glomerata*, and *C. pentagona* revealed no indication of nuclear or cell division from the time a root emerges from the seed until it has reached its full length (about 1-1½ cm). These observations and the comparatively close similarity of the root portion of the long, coiled, dormant embryo to the peculiar root (Hooker, 1898) developed from it make it appear likely that all the cells of the root are present in the embryo when the seed reaches maturity. However, it still remains possible that some divisions may occur between the beginning of activity of the embryo and the time that the root appears through the seed coat.

Somatic mitoses were studied to some extent in stem tips, young buds, and in a few cases in the early stages of haustorium-formation, but because of the difficulty of finding satisfactory division figures in these places the study was confined largely to the divisions of the microspore mother cells.

#### *C. Gronovii* Willd. $n = 30$

The seeds from which plants of this species were grown were collected in the University Arboretum in the fall of 1936. *Impatiens Sultani* Hook. and *Coleus Blumei* Benth. var. *Renhaltianus* proved satisfactory hosts. Growth was slightly less vigorous on common geranium (*Pelargonium hortorum* Bailey). No cytological difference was observed between material grown on these different hosts, but since all allowed a normal growth of the dodder the possibility of cytological abnormalities in plants drawing their substance from more unfavorable hosts is not excluded. Kindermann (1928) reports amitosis in a large haustorial cell of *Cuscuta Gronovii* growing poorly on *Nicotiana rustica* and attributes it to the unfavorable action of materials taken from the host. One case of apparent amitosis was observed in this species in the present study, although the host (*Impatiens Sultani*) appeared to be in no way unfavorable. The cell in which it occurred was one of the system of large lactiferous cells (Peirce, 1893) which runs through the whole plant, this one being in a petal.

Microspore-mother-cell nuclei at diakinesis (fig. 4) possess 30 mostly well-separated chromosome pairs which can be counted without great difficulty if stained with Flemming's triple stain or with crystal violet-iodine. With these stains the nucleolus is differentiated so that it does not hinder the distinguishing of the 4, 5, or 6 pairs that are commonly clustered

about that body. Most of the pairs lie in the peripheral region of the nucleus. In some preparations delicate strands are observed to connect many of the pairs with one another.

Although about six of the pairs have only one chiasma each in most late diakineti nuclei and some pairs occasionally show more than two chiasmata (the interstitial one and sometimes one of the terminal ones in these cases appearing as delicate strands), the chromosomes of the majority of the gemini at this stage are in contact at both ends and are comparatively widely separated in the intermediate region. This condition, developing from a diplotene and early diakineti condition in which the average number of points of contact between members of the pairs is certainly greater, may be interpreted as the result of terminalization of chiasmata (Darlington, 1932).

One of the V-shaped pairs (*a*, fig. 4) is conspicuously heteromorphic. Besides characteristic differences in outline between the two members, one of them is about  $1.6\mu$ , the other about  $2.3\mu$  long. This pair and about 6 others can be identified with a fair degree of assurance in many diakineti nuclei. Identifications correlative with these have not yet been made in earlier stages, but the distinctive appearance of some of the diakineti pairs suggests that possibility.

In most heterotypic equatorial plates (fig. 1) connecting strands are evident between a number of the chromosome pairs which are far enough apart in the plates to allow a view of such structures. The presence of these suggests that the strands, mentioned earlier as being visible in some diakineti nuclei, remain as the chromosomes pass to the equatorial plate, becoming shorter along with the chromosomes. The chromosome pairs at the heterotypic equatorial plate vary from nearly spherical (with a diameter of  $1\mu$  to  $1.8\mu$ ) or angular and approximately isodiametric to somewhat elongated with the longest axis of any pair not found to exceed  $2.2\mu$ .

The chromosomes in the homoeotypic equatorial plates are more angular, generally more widely separated, without connecting strands, and, of course, smaller than are the pairs of chromosomes at the heterotypic equatorial plate.

A nucleolar bud, about  $1.4\mu$  in diameter, with a satellited chromosome pair associated with it at its base (fig. 3), was observed in a microsporocyte nucleus apparently in a pachytene stage. Such buds are typically present in this species, but the associated satellite chromosome cannot from the observations made be said to be a constant feature.

While the nucleolar bud just described is fairly typical as to size and form, variations appear in size, number, and relative position of buds on

the nucleolus. A bud or buds may or may not be present at a particular stage. An unusual size variation is shown in figure 2, where the "bud" is almost as large as the main body of the nucleolus. In a relatively large number of diakinetic nuclei two buds have been observed on a single nucleolus, these most often being 180° apart and usually each having a pair of chromosomes (not visibly satellited) in contact with it. The nucleolus shown in figure 4 bears two buds about 90 degrees apart, each having a chromosome pair directly above and apparently in contact with it.

Some tapetal nuclei undergo mitosis when the microsporocyte nuclei are in synizesis. A slightly greater number of these tapetal divisions is seen just after synizesis. All the tapetal cells normally become binucleate, and the majority of them remain in that condition until the cells and finally the nuclei disintegrate during the growth period of the microspores. The time at which the majority of the tapetal cells become binucleate is slightly later than that reported in *C. reflexa* Roxb. (Johri 1935). Frequently several of the tapetal cells of a locule are 4-nucleate at the time the pollen-mother-cell nuclei are in diakinesis, and in a few rare cases tapetal cells with 6 or 8 small nuclei are seen.

The nuclei of all somatic cells in the metabolic condition show chromocenters. Exact counts of these were not found feasible, but in some cases it appears that the number about equals the number of chromosomes (60). In other cases, however, the number of chromocenters is much less.

#### *C. Cephalanthi* Engelm. $n = 30$

The 30 pairs of chromosomes which constitute the heterotypic equatorial plate (fig. 7) of this species are similar to those of *C. Gronovii* in size as well as in number. A tendency for more of the pairs to appear biscuit-shaped in polar view than in *C. Gronovii* is not so pronounced in the plate shown as in many of the others seen. Whether this slight difference between the two species is due only to the orientation of the equatorial-plate chromosomes, or whether there is an actual difference in the form of the chromosomes, could not be ascertained by a study of lateral views of equatorial plates. The threads connecting several of the pairs in the heterotypic equatorial plate are interpreted as in *C. Gronovii* to be structures which existed in earlier stages and which have persisted. These threads are not seen in the homoeotypic equatorial plate (fig. 6).

The most conspicuous cytological difference between this species and *C. Gronovii* is found in the appearance of the chromosomes at diakinesis. Whereas in the late heterotypic prophase of *C. Gronovii* there is a relatively long period during which 30 distinct and well-separated pairs of chromosomes are found, *C. Cephalanthi* shows from about 15 to 21 as-

sociations of chromosomes some of them evidently groups of four (fig. 9). One such group from a nucleus at a slightly earlier stage (fig. 10) is shown which appears to consist of two chromosomes in a ring and (probably) two others attached. To insure against the possibility that nuclei or portions of nuclei of an earlier stage (diplonema and early diakinesis) were being

#### Explanation of plate 32

All drawings were made at a magnification of  $\times$  ca. 2000 with the aid of a camera lucida.

Fig. 1. Heterotypic equatorial plate of *C. Gronovii*;  $n=30$ .

Fig. 2. Nucleolus with large bud and associated chromosomes, from a post-synizetic pachytene nucleus of *C. Gronovii*.

Fig. 3. Satellite chromosome pair associated with a nucleolus and bud in a nucleus similar to that from which figure 2 was drawn.

Fig. 4. Nucleus of *C. Gronovii* pollen mother cell with 30 pairs of chromosomes at diakinesis.

Fig. 5. Pair of apparently satellite chromosomes from a pollen mother cell nucleus of *C. Gronovii* at diakinesis.

Fig. 6. Homoeotypic equatorial plate of *C. Cephalanthi*;  $n=30$ .

Fig. 7. Heterotypic equatorial plate of *C. Cephalanthi*.

Fig. 8. Optical section of a pollen mother cell of *C. Cephalanthi* in a late homoeotypic prophase showing one of the groups of chromosomes scattered on a multipolar spindle. Circles represent extra-nuclear nucleoli.

Fig. 9. Three apparently tetravalent chromosome groups from a mid-diakinetic nucleus of *C. Cephalanthi*.

Fig. 10. Apparently tetravalent chromosome group in *C. Cephalanthi* at a slightly earlier stage than that of figure 9.

Fig. 11. Heterotypic equatorial plate of *C. glomerata*;  $n=15$ .

Fig. 12. Heterotypic equatorial plate of *C. compacta*;  $n=ca. 15$ .

Fig. 13. Homoeotypic equatorial plate of *C. pentagona*;  $n=ca. 28$ .

Fig. 14. Homoeotypic equatorial plate of *C. campestris*;  $n=28$ .

Fig. 15. Heterotypic equatorial plate of *C. Coryli*;  $n=15$ .

Fig. 16. Equatorial-plate chromosome from a cell of a petal of *C. Coryli*.

Fig. 17. Equatorial-plate chromosome  $16\mu$  long from a cell of a petal of *C. indecora* var. *neuropetala*.

Fig. 18. Satellite chromosome from same plate as figure 17.

Fig. 19. Satellite chromosome near nucleolus; prophase in a tapetal nucleus of *C. Cephalanthi*.

Fig. 20. Heterotypic prophase nucleus of *C. campestris* with dark-staining portion in nucleolus in contact with a chromosome.

Fig. 21. Similar to figure 20. Different view.

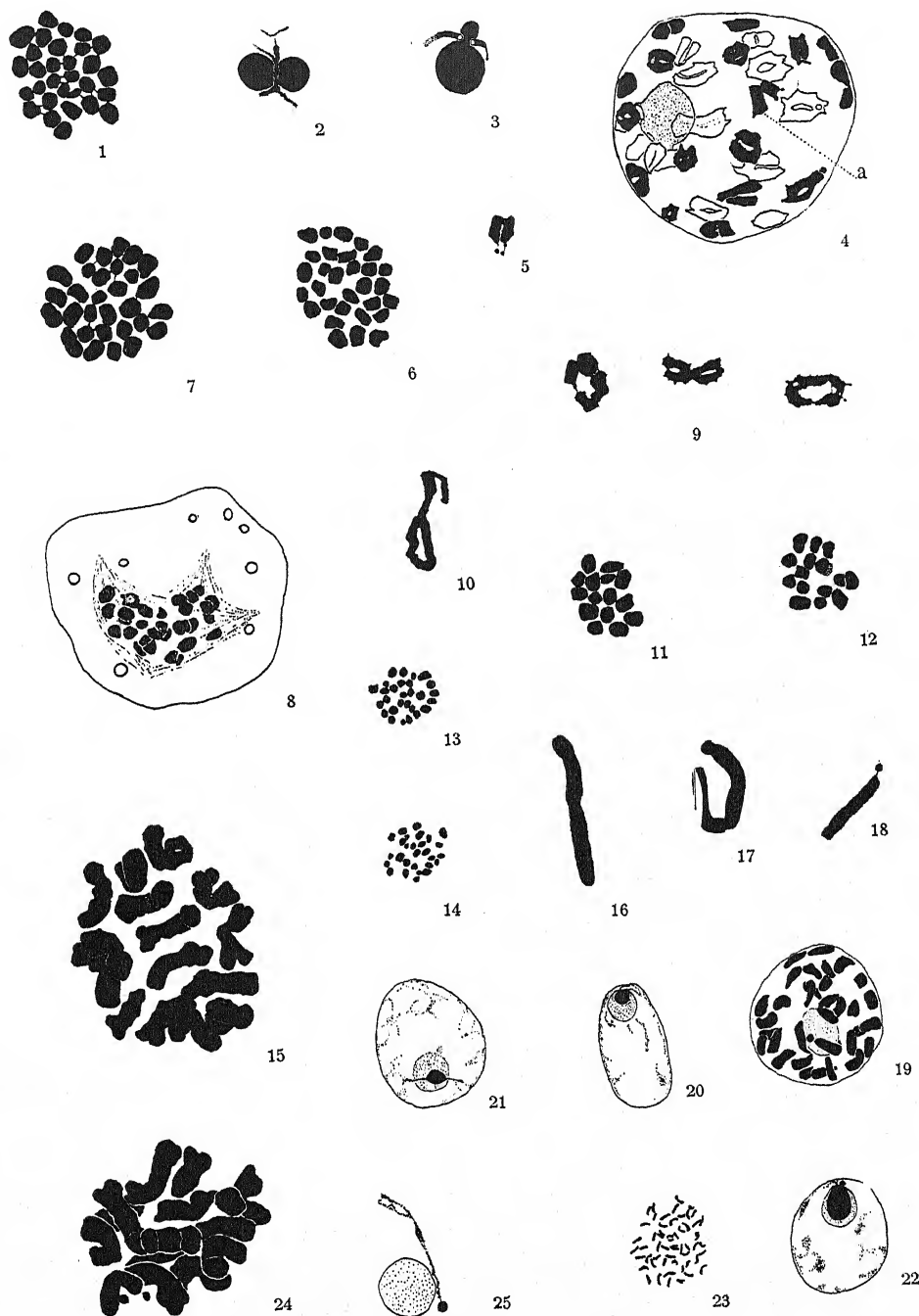
Fig. 22. Similar to figures 20 and 21; an earlier stage.

Fig. 23. Equatorial plate from a cell of an ovule primordium in *C. campestris*;  $2n=56$ .

Fig. 24. Heterotypic equatorial plate of *C. indecora neuropetala*;  $n=15$ .

Fig. 25. Large satellite on chromosome in contact with nucleolus in an early heterotypic prophase in *C. indecora neuropetala*.





FOGELBERG: CUSCUTA

compared with the stage of *C. Gronovii* shown in figure 4 (middle or late diakinesis), a large amount of material was cut at a sufficient thickness ( $28\mu$  and  $30\mu$ ) to give a high incidence of whole nuclei at all possible stages. In one nucleus in which the nucleolus had disappeared and the nuclear membrane was not evident, about 24 separate groups of chromosomes were counted. Some of these had taken on the smooth outline and contracted appearance of chromosome pairs moving toward the equatorial plate. The rather disorganized orientation and distribution of the chromosome pairs or groups in this nucleus made impossible the interpretation of a large proportion of them or even the reliable counting of the number of actually separate associations.

The tapetal cells become binucleate in this species, as in *C. Gronovii*, to some extent while the microsporocyte nuclei are in synizesis but mostly just after synizesis. In this species, too, a small number of the tapetal cells become 4-nucleate. The second tapetal nuclear division occurs usually while the microsporocyte nuclei are at about the diplotene stage. Preparations suggesting fusions of tapetal nuclei at the time the microspores are in tetrads are not uncommon.

In a few locules in which the microsporocyte nuclei had undergone the heterotypic division the chromosomes were scattered on multipolar spindles (fig. 8, showing one of the two spindles in the cell). Two interpretations are possible from the appearance of these preparations. Either these spindles are the result of abnormal conditions in the genetic constitution or environment of the plant and would probably result in the formation of more than 4 microspore nuclei in each cell; or they are a normal stage preceding the formation of the bipolar spindles, as is the case in the heterotypic division in various other plants. The second interpretation is favored here because no evidence of abnormality was seen in other locules of the anthers or in other anthers of the flowers in which these multipolar homoeotypic spindles occurred. The microspores and pollen grains, too, appear from their size and staining reactions to be entirely normal in this species.

Extra-nuclear nucleoli of various sizes are abundant in the microsporocytes of this species (fig. 8) as well as in *C. Gronovii*. These bodies become apparent in the cytoplasm when the nucleolus and nuclear membrane have disappeared in preparation for the heterotypic division. They are spherical or nearly so in shape, generally less than  $1\mu$  in diameter, and stain in the same manner as ordinary nucleoli with Flemming's triple, crystal violet-iodine, and Heidenhain's iron-alum haematoxylin stains.

*C. glomerata* Choisy  $n=15$ 

The seeds from which this species was grown were collected near Madison. *Aster* sp. was used as a host.

The average size of chromosomes in this species (fig. 11) is slightly larger than in the two preceding. The nuclei at diakinesis possess pairs of chromosomes most of which have 2 terminal chiasmata and rather widely separated intermediate portions. The chromosomes were counted in the heterotypic and homoeotypic equatorial plates and in the homoeotypic prophase. The latter stages are very satisfactory for counting, for although the chromatids often diverge widely the chromosomes are generally separated and distinct.

Fixation of buds of this species, in order to be successful, must be preceded by removal of the many papery bracts.

*C. compacta* Juss.  $n=ca. 15$ 

The fifteen pairs of chromosomes in this species (fig. 12) are similar to those of *C. glomerata*. The average size of the chromosome pairs in the heterotypic equatorial plate is about  $1.5\mu$  by  $1.75\mu$ . Cytological study is made difficult by large quantities of a substance (perhaps tannin) which darkens when the cells are fixed. The chromosomes have been counted only in heterotypic equatorial plates and in some homoeotypic plates which were all questionable in certain portions. Hence the number is not positively determined, but it appears to be that given.

*C. pentagona* Engelm.  $n=ca. 28$ 

Seeds of this species were collected by Prof. Yuncker near Greencastle, Indiana, in 1936. One of the three instances of hosts proving definitely unfavorable was found when this species was tried on *Tropaeolum majus*. After growing slowly on this host for about 8 weeks, a few flowers were produced. When growing tips of the dodder were placed on plants of *Pelargonium hortorum* a 5-week period of vegetative growth followed after which an abundance of flowers appeared.

The minuteness of chromosomes of this species and of the very similar *C. campestris* offers difficulty in the counting. The average size of the chromosomes in the homoeotypic equatorial plate (fig. 13) is about  $0.5\mu$  by  $0.7\mu$ , and in the heterotypic equatorial plate  $0.7\mu$  by  $0.8\mu$ . The somatic chromosomes vary in length from about  $0.4\mu$  to  $1.2\mu$ .

*C. campestris* Yuncker  $n=28, 2n=56$ 

The seeds from which material of this species was grown were taken from a specimen in the herbarium of the Missouri Botanical Garden col-

lected at Langley, Arkansas, in 1933. Professor Yuncker verified the identification.

The species was studied by Finn and Safijovska (1934) and their counts are here confirmed. Figure 14 shows 28 chromosomes in a homoeotypic equatorial plate, and figure 23 about 56 chromosomes in a somatic plate.

No marked cytological difference between this species and *C. pentagona* was observed. A portion of the interior of the nucleolus stains more deeply than the rest in iron alum-haematoxylin material destained until prophase chromosomes are only faintly visible (figs. 20, 21, 22). This darkly stained portion of the nucleolus is connected with a chromosome pair throughout the prophases of the heterotypic division. This darker-staining portion varies considerably in size in different pollen sacs, but the nucleoli in a given sac present little variation. In all cases the darker portion is eccentrically located. The constant location, the connection with a chromosome pair, and the sharply defined outline of this portion of the nucleolus, as well as the fact that in different locules of the same preparation the darker portion varies considerably in size, indicate that the variation is not due to different degrees of destaining.

*C. Coryli* Engelm.  $n = 15$

This species was grown on *Tropaeolum majus* and to some extent on the garden pea. On *Coleus* it behaved in the manner described for *C. pentagona* on *Tropaeolum*.

This species has much larger chromosomes than any of those previously mentioned. Those of the longest pair in the heterotypic equatorial plate (fig. 15) are about  $8\mu$  in length, the shortest about  $4\mu$ . The diameter varies considerably, from about  $1\mu$  to more than  $2\frac{1}{2}\mu$ , and the outlines of the chromosome pairs are rough and irregular. A constriction or a clear space marking the fiber-attachment region is visible in some of the chromosomes. Lateral views often show the chromosomal material at the fiber-attachment region drawn out to a point on either side.

Since several of the chromosome pairs are very similar, I have not attempted to identify all. However, certain pairs can usually be recognized in different heterotypic equatorial plates. Two V-shaped pairs about  $7\mu$  long and conspicuously double at both ends are commonly seen, and one (occasionally both) of these shows a median clear region. The longest pair has a thicker portion between the median, constricted region and one end. A short pair ( $4\mu$  long) usually appears double at one end, tapering to a blunt point at the other. This peculiar chromosome appears also in the species next to be mentioned.

Nucleolar buds of varying size were seen in heterotypic prophase. In some diplotene nuclei a chromosome is in contact with the nucleolus at the base of a bud. In others no chromosome is seen near the bud. The relative length and a marked clear region near the opposite end of each chromosome of the attached pair may identify it with one of the pairs seen in somatic cells which agree in these characteristics and which possess a satellite on the end farther away from the clear region. A study of somatic prophase might establish this identity more definitely. A tapetal cell with more than two nuclei has never been observed in this species or in *C. indecora* and many of them remain uninucleate throughout their existence.

The seeds from which this species was raised were taken from a specimen collected at Wonewoc, Wisconsin, in 1917. Since old seeds have been shown in some cases to give rise to plants showing a greater number of genetic and chromosomal mutations and mitotic irregularities (Crocker, 1938) than do younger seeds, evidence of irregularity was looked for in this plant. In an appreciable number of cases sister chromosomes were observed to be not completely separated at full anaphase, *i.e.*, when the daughter groups were as far apart as they would ever be. Similar conditions were occasionally observed in heterotypic and homoeotypic anaphases as well as in somatic divisions. However, the mechanical difficulties in the separation of such extremely long chromosomes as are present in this and the next species may account for the few instances indicating irregularity which have been observed. The pollen appears to be almost completely normal.

*C. indecora* var. *neuropetala* (Engelm.) Hitchcock  $n=15$

The seeds of this variety were taken from a Gray Herbarium specimen collected at Ashley, North Dakota, in 1934. *Pelargonium* was used as a host, since it allowed a more luxuriant growth than the other hosts tried (*Coleus*, *Convolvulus*). The *Pelargonium* formed a conspicuous gall in response to the penetration of the first few haustoria, smaller ones later.

This variety has not been as extensively studied as has *C. Coryli*, but the counts of heterotypic (fig. 24) and homoeotypic equatorial plates indicate that 15 is the haploid number and that the chromosomes are similar to those of *C. Coryli*. Besides the peculiar short chromosome pair mentioned for *C. Coryli*, which is very similar to one in the present species, several others may possibly be identified in the two species by further study. The chromosomes of the satellite pair (fig. 18) in *C. indecora* var. *neuropetala*, though, are considerably shorter than the members of the satellite pair in *C. Coryli* and lack the broad clear region seen in the latter



case. Measurement of one of the larger somatic chromosomes (fig. 17) seen in the equatorial plate shows it to be about 16 or 17 $\mu$  in length, the largest observed in the genus.

#### DISCUSSION

The eight species studied fall into four rather widely separated groups representing five of the twelve sub-sections of the section *Cleistogrammica*, sub-genus *GRAMMICA*. In general, the cytological evidence in regard to phylogenetic relationships within and among the sub-sections investigated agrees with the scheme based on morphological characters which Yuncker (1932) has suggested. Certain exceptions, however, may be pointed out.

According to Yuncker the sub-section *Cephalanthae*, containing only *C. Cephalanthi*, is probably derived from the sub-section *Oxycarpae*. To the latter sub-section, which includes *C. Gronovii* and its two recognized varieties, belong also *C. curta* (Engelm.) Rydberg and *C. rostrata* Shuttleworth. These two species do not approach *C. Cephalanthi* as closely in morphological characters as does *C. Gronovii*. Hence, if the ancestor of *C. Cephalanthi* is to be looked for among extant representatives of this sub-section, *C. Gronovii* and its varieties appear from morphological evidence to be the only likely possibilities. The chance that the varieties of *C. Gronovii* differ cytologically from the typical form appears slight from what is known concerning closely related species in the genus as well as of similar cases in other genera. The behavior of the chromosomes in diakineti-  
c nuclei of *C. Cephalanthi* and *C. Gronovii* is hardly consistent with the idea that the latter species is the ancestor of the former, since it is unlikely that so many tetravalent associations would have developed among chromosomes which had once formed only bivalents at this stage. Another possibility is that the two species have resulted from a parallel development. If both originated from types with 15 pairs of chromosomes, then it would seem likely either that *C. Gronovii* is an allotetraploid or that the original pairs of homologous chromosomes have developed enough genetical differences since the origin of this plant so that now little evidence of multivalent association is seen. On the other hand, the occurrence of tetravalent chromosome associations in *C. Cephalanthi* suggests that it may well be an autotetraploid. In any case, the similarity between the two species in cytological details, in external morphology, and in geographical distribution indicates that their ancestries converge at a relatively nearby point in the phylogenetic system.

The sub-section *Lepidanche*, which includes *C. glomerata* and *C. compacta*, is suggested by Yuncker as being derived from the subsection *Oxycarpae* (including *C. Gronovii*). Cytological evidence of such relation-

ship has not been found. However, if some representative of the Oxycarpae should be found to have 15 pairs of chromosomes, a possible line of development would be evident. *C. rostrata* appears somewhat more closely related to the sub-section Lepidanche than others of the Oxycarpae. The chromosomes of *C. Gronovii* and *C. Cephalanthi* do not differ markedly from those of *C. glomerata* or of *C. compacta* in size or form, suggesting a possible fairly close relationship.

None of the forms studied is in the suggested line of ancestry of the sub-section Indecorae, in which *C. Coryli* and *C. indecora* var. *neuropetala* are placed. A comparison of the average chromosome size in these two as compared with other species in the genus (especially *C. campestris* and *C. pentagona*) shows a range of divergence which is unusual within a genus. As Yuncker's (1932) diagram indicates, these two related species probably fall in a different line of development from any of the others investigated. Finn and Safijovska (1934) pointed out the great difference in chromosome size between *C. monogyna* and other species studied by them and cite the work of Heitz (1926). Heitz found great variation in average chromosome size between species of *Cyclamen*, those with larger chromosomes having in every case a more northerly distribution. Although the two large-chromosomed species of *Cuscuta* (*C. Coryli* and *C. indecora neuropetala*) do occur farther north (both occurring in North Dakota and *C. Coryli* in central Wisconsin) than a majority of the species in the genus, it appears more significant in this case that it is the two species with 60 medium-sized chromosomes which range farther north than do any of the others. Several cases have been pointed out (Hurst, 1927; Anderson, 1937) in which the members of a polyploid series possessing the higher chromosome numbers have the more northerly ranges.

Another apparently distinct line of evolution among the American species of dodder is that which has given rise to *C. pentagona* and *C. campestris*. The form and extremely small size of the chromosomes and the existence of a different basic number in these two species sets the sub-section Arvenses apart from all others studied. The fact that these species have 28 pairs of chromosomes rather than some multiple of 15 as do the others studied is probably correlated with the occurrence of polyploid series with the basic number 7 in certain representatives of the sub-genera CUSCUTA and MONOGYNA.

In the section Eucuscuta of the sub-genus CUSCUTA, Finn and Safijovska find two species with a haploid chromosome number of 7 and one with a haploid number of 21. If this section does represent the present climax of one line of development within the genus, as Yuncker's suggested scheme indicates, then it seems improbable that some of the representa-

tives of the intermediate and most primitive groups too do not possess a haploid number of 7. However, the possibility remains that such forms, formerly existent, may have disappeared.

In the sub-genus MONOGYNA, which is suggested to have developed as an offshoot from forms of the sub-genus CUSCUTA which preceded the section Eucuscuta in phylogeny, only *C. monogyna* has been investigated cytologically. Finn and Safijovska (1934) report this species to have 14 pairs of rather large chromosomes. If the true line of development of the sub-genus is that suggested, there is an indication that forms with a small number of chromosomes and with a basic number of 7 do exist or have existed in the more primitive groups of this sub-genus.

#### SUMMARY

The evidence indicates that all the cells of the mature root of a dodder seedling are present in the dormant embryo.

The following chromosome numbers are reported:

- C. Gronovii* Willd.  $n=30$ ;
- C. Cephalanthi* Engelm.  $n=30$ ;
- C. glomerata* Choisy  $n=15$ ;
- C. compacta* Juss.  $n=ca. 15$ ;
- C. Coryli* Engelm.  $n=15$ ;
- C. indecora neuropetala* (Engelm.) Hitchcock  $n=15$ ;
- C. pentagona* Engelm.  $n=ca. 28$ ;
- C. campestris* Yuncker  $n=28, 2n=56$ .

*C. Gronovii* and *C. Cephalanthi* have chromosomes similar in size but differing in their behavior in meiosis; those of *C. Gronovii* forming 30 separate pairs and many of those of *C. Cephalanthi* appearing in groups of four. A satellite chromosome pair is present in association with the nucleolus, often attached at the base of a nucleolar bud, in *C. Gronovii*. The tapetal cells in both species become binucleate during or just after synizesis.

*C. glomerata* and *C. compacta* have chromosomes similar to those of *C. Cephalanthi* and *C. Gronovii*.

The chromosome pairs in the heterotypic equatorial plate in *C. Coryli* and in *C. indecora neuropetala* are relatively very large, varying from  $4\mu$  to  $8\mu$  in length. Distinctive sizes, constrictions, and achromatic regions allow the identification of several of the pairs from one equatorial plate to another in *C. Coryli* and probably in *C. indecora neuropetala* as well. Certain chromosomes of either correspond in size and morphology with chromosomes of the other species.

*C. campestris* and *C. pentagona* have extremely small chromosomes;

the difference in average chromosome size as between these and the two very large-chromosomed species previously mentioned is unusual in a single genus of plants.

Certain suggestions regarding relationship of species within the genus are furnished by the cytological facts available.

The writer wishes to express his gratitude to Professor C. E. Allen for criticisms and suggestions.

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## New Florida Polypores

W. A. MURRILL

(WITH FIVE FIGURES)

Central Florida abounds in polypores and the meeting of the northern and tropical species in this region never fails to interest the student. For example, *Hexagona alveolaris* fades out and *H. daedalea* becomes abundant; *Daedalea quercina* is nowhere to be seen, while *D. ambigua* is everywhere; our old northern friend, *Elfvigia applanata*, disappears but *E. marmorata* more than fills its place, while *E. tornata* creeps in sparingly from the tropics. Of *Polyporus polyporus* there is none, but *P. arcularius* springs from every buried stick, often associated with the brilliant sporophores of the tropical *Pycnoporus sanguineus*.

In this middle ground there must be some more or less local species, and a few of these have not heretofore been recognized. There are also a few rare enough or interesting enough to deserve special mention.

### TRAMETES AMYGDALINA (Berk. & Rav.) Murrill

*Polyporus amygdalinus* Berk. & Rav.; Berk. Grevillea 1: 49. 1872.

My first real knowledge of this interesting species dates back about twenty years, when Dr. R. P. Burke sent it to me from Alabama. On Dec. 14, 1926, I first collected it at Gainesville; and on June 8, 1930, it was collected by Mr. Erdman West, Mycologist of the Florida Agricultural Experiment Station. These specimens were all old or dried when I first saw them, not exhibiting the true beauty of the fresh plant. In contrast to *Laetiporus sulphureus*, which it greatly resembles, the hymenophores may persist for months *in situ*, simply drying and fading, because the context is too tough to be attractive to insects or other enemies.

My first acquaintance with fresh plants was on Mar. 25, 1938, at Gainesville, when I found two fine hymenophores on old oak logs imbedded in wet soil in a low hammock. One had just reached maturity, while the other showed the milk-white tubes just forming. Both were about six by nine inches, two inches thick behind, with the tumid margin pale orange without and within, and the uneven, zonate surface umbrinous-fulvous near the margin and umbrinous behind. On first sight one could not fail to think of *L. sulphureus*; but, noting the dark color of the older portion of the pileus, further investigation would reveal the tough context and the difference in spore characters.

### ELFVINGIA TORNATA (Pers.) Murrill

This common tropical species, closely allied to *Ganoderma*, has been

familiar to me for nearly forty years, but I was hardly prepared to find it in Central Florida. Although rare here, it has a wide range of hosts, extending even to orange and pine. The northerner would undoubtedly pass it by for the common *Elfvigia applanata*, but the surface is hard and the spores rough. Its favorite host in this region seems to be oak, either living or dead. I found it on orange in 1927, but Mr. Rhoads had collected it on this host two years before near Mt. Dora, and Dr. W. B. Tisdale on orange at Groveland, in 1932. My greatest surprise was at Green Cove Springs on Mar. 10, 1926, when I saw it growing on the stump of a slash pine that had been cut two years previously. The hymenophores were imbricate, the largest eight inches broad, and attached both to stump and roots.

PORIA VINCTA (Berk.) Cooke

Described from Santo Domingo and found generally throughout tropical regions. At Gainesville it is fairly common on rotting logs of oak, magnolia, sweet gum and other broad-leaved trees, usually staining the wood orange. The northern mycologist would probably call it *P. attenuata* Pk. or *P. eupora* P. Karst. because of its rosy-isabelline color, but closer investigation reveals certain well-defined differences. I find the spores to be subglobose to broadly ellipsoid, smooth, hyaline, not guttulate,  $3-4 \times 2-3\mu$ , about as in *P. attenuata*, but there are no cystidia.

SCUTIGER PERSICINUS (Berk. & Curt.) Murrill

This rare species, previously collected only in pine woods, was found by the author on June 14, 1938, at Gainesville, Fla., growing up between the roots near the base of a large live-oak. The following notes were made from the fresh specimens: Circular or irregular, somewhat lobed, 10-17 cm. broad, convex to depressed, rough, uneven, short-tomentose, white to rosy-isabelline, then bay or chestnut, blackening where bruised; margin tumid, white at first and remaining paler than the rest of the surface; context 2-3 cm. thick, zonate, white, changing to rosy-isabelline at once when cut and growing gradually darker; tubes decurrent, very short and small, white, becoming bay when bruised; stipe central, subcylindric, tomentose, white to umbrinous, darker with age or where bruised, about  $8 \times 4$  cm.

Mr. Erdman West collected an older specimen under an oak near Gainesville on June 30, 1938, which measured  $18 \times 14$  cm. It was irregularly elliptic with undulate margin, blackish on the disk, and the remainder either castaneous or atropurpureous; hymenium white with a suggestion of pink, becoming purple where bruised; spores copious, ellipsoid, smooth, hyaline,  $5-7 \times 3-4\mu$ . It may be that this is an oak-loving species after all, probably attacking the roots of its host.

MICROPORELLUS MUTABILIS (Berk. & Curt.) Murrill, comb. nov.

*Polyporus mutabilis* Berk. & Curt. Ann Mag. Nat. Hist. II. 12: 433. 1853.

This species is common about Gainesville on fallen dead hardwood branches in low ground. It is thin, zonate, and regular or irregular, the spores being globose to ovoid, smooth, hyaline, uninucleate, not apiculate, about  $3-4 \times 2.5-3 \mu$ . It is also common in tropical America.

*M. dealbatus* (Berk. & Curt.) Murrill, formerly considered rare, has been collected here frequently during recent months. It never grows on the top of dead branches, but springs up from decayed roots, and is an annual. Thicker, whiter, and more regular than *M. mutabilis*, it has spores that are irregularly broadly ellipsoid, conspicuously obliquely apiculate, smooth, hyaline, granular, thin-walled, and about  $4 \times 3 \mu$ . Its range seems to be from central Florida through the Carolinas to Kentucky and Missouri.

AURANTIPORUS CROCEUS (Pers.) Murrill, comb. nov.

*Polyporus croceus* Pers. Obs. Myc. 1: 87. 1796.

Mr. Erdman West found a very handsome specimen of this rare and interesting species in a hammock near Gainesville, Fla., August 4, 1938 (F17982). It grew on the base of a giant living live-oak and was fully a foot wide. The surface was partly reddish-orange but mostly ochraceous; the context beautifully concentrically zonate; and the slender bright-orange tubes, over 2 cm. long, had just reached maturity. Near this tree, on the top of a dead oak log, another hymenophore was just beginning to form. In western North Carolina I found the fruit-bodies growing on the sides of oak and chestnut logs that were much decayed.

NIGROPORUS VINOSUS (Berk.) Murrill

Described from Santo Domingo and known also from Cuba and the State of Georgia. I have found it twice on pine wood and once on *Nyssa* in the vicinity of Gainesville, Fla.; and in July, 1938, Dr. G. F. Weber got a fine collection here of large specimens on a pine log. In the region about Gainesville it is frequent on dead logs of both hardwoods and pine. In the fresh condition it is easily confused with *Fomes subroseus*. Saccardo's "Sylloge," 1925, lists *Polyporus badius* Jungh. as a synonym.

Daedalea Westii sp. nov.

Pileo effuso-reflexo, 10-15 cm., tomentoso, ochraceo; poris 1-1.5 cm. longis, ochraceis, demum lacerato-dentatis.

Hymenophore effused-reflexed, simple or terraced-imbricate, growing in a narrow strip 15 cm. long or covering a spot on the trunk about 10 cm square;



Fig. 1. *Polyporus Westii* Murrill, Type collection (F18100)  $\times \frac{1}{2}$ , in Florida Agricultural Experiment Station Herbarium.  
Photo by A. S. Rhoads.

the reflexed portion triangular in section,  $1-1.5 \times 2-3 \times 1-1.5$  cm., broader by confluence; surface tomentose, uneven, azonate, ochraceous to isabelline, margin undulate; context corky, homogeneous, white, about 5 mm. thick; tubes labyrinthiform, 1-1.5 cm. long, pallid within, edges obtuse, uneven, ochraceous, entire to lacerate-dentate; cystidia lacking; spores not found.

Type collected by Erdman West on living red cedar at Gainesville, Fla., Sept. 15, 1936 (No. *F9190*<sup>1</sup>). Also collected by A. S. Rhoads on the same host at Clemson College, S. C., Aug. 27, 1936 (No. *F8754*). The latter collection represents an older stage in the development of the hymenophore and was used in making the description more complete. This species shows no resemblance to *D. juniperina*, which is ungulate in form and much larger, although the descriptions sound much alike.

*Pyropolyporus taxodii* sp. nov.

Pileo dimidiato,  $6 \times 10 \times 2.5$  cm., tomentuloso, zonato, fulvo; poris parvis, castaneo-umbrinis.

Pileus dimidiate, appanate, sessile by a rather broad base, solitary,  $6 \times 10 \times 2.5$  cm.; surface densely tomentulose, uneven, zonate to sulcate, fulvous, bay on two of the very narrow bands, margin subacute, undulate to slightly lobed; context hard, woody, indistinctly concentrically zonate, about 1 cm. thick, ferruginous-ochraceous, subshining; tubes unstratified, reaching about 1 cm., 5 to a mm., thick-walled, isabelline-avellaneous within, mouths circular, edges entire, slightly glistening, castaneous-umbrinous; cystidia absent; spores not found but doubtless hyaline.

Type collected by A. S. Rhoads on a dead standing pond cypress at Gainesville, Fla., Nov. 11, 1923 (No. *F16254*). An attractive and interesting species found but once. Described from the dried specimen.

*Polyporus Westii* sp. nov.

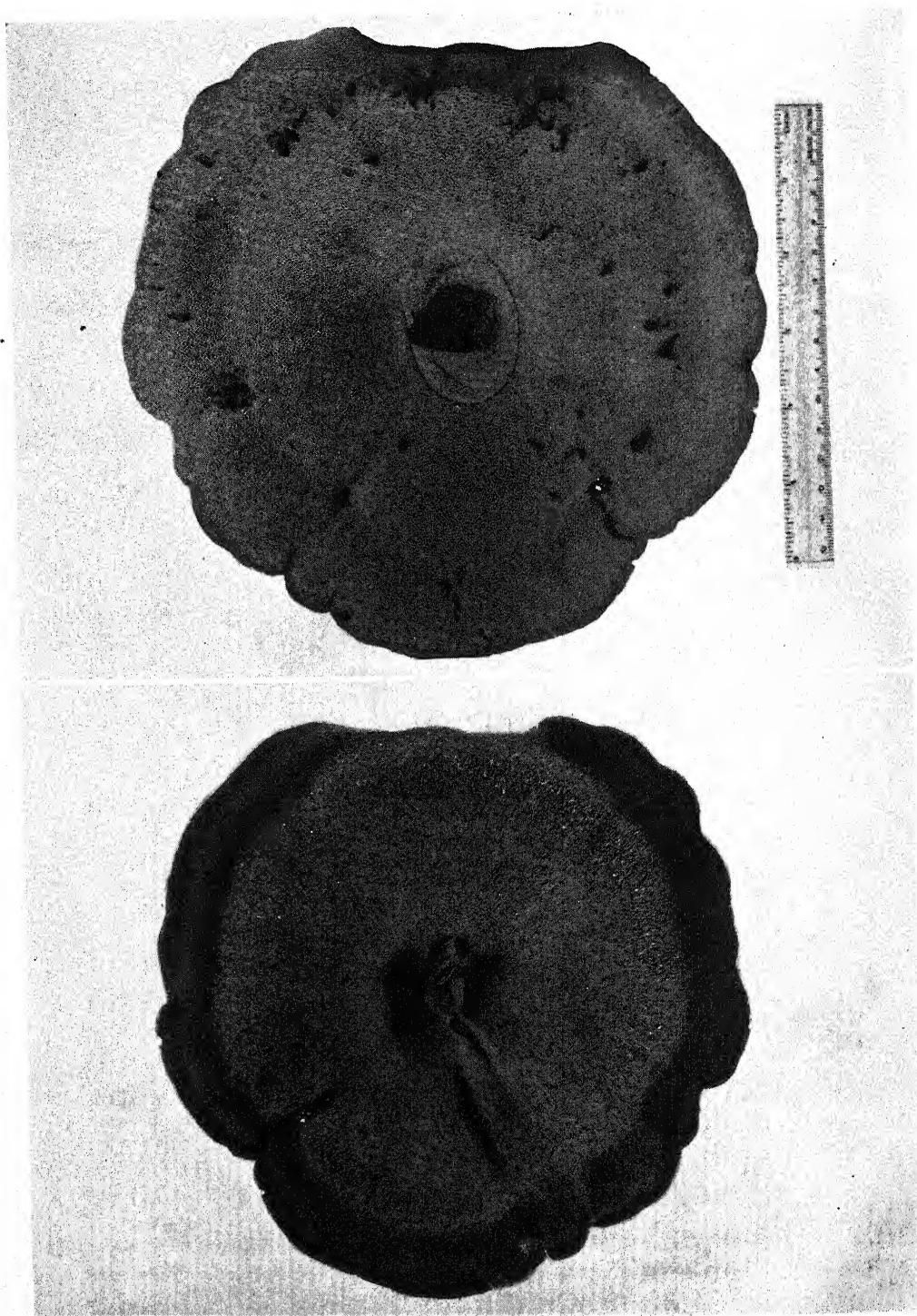
Pileo infundibuliformi, 7-20 cm. lato, umbrino, hispidello, reticulato, lobato, 1-2 cm. crasso; tubulis angulatis, sporis hyalinis,  $10-12 \times 4-5\mu$ ; stipite tomentoso,  $4 \times 3$  cm.

Pileus somewhat irregular, infundibuliform, solitary, 7-20 cm. broad; surface umbrinous, finely hispid, reticulate; margin fuliginous, deflexed, lobed; context soft, white, sweet and nutty, 1-2 cm. thick; tubes decurrent, about 3 mm. long, 1 to a mm., white, angular, the edges very thin, entire; spores elongate, granular, smooth, hyaline,  $10-12 \times 4-5\mu$ ; stipe pale-avellaneous, tomentose, umbrinous at the base, about  $4 \times 3$  cm.

Type collected by West, Rhoads, Wodehouse and Murrill on the top of a rotten sweet-gum log in Planera Hammock, eleven miles northwest of

<sup>1</sup> All of the specimens cited in this paper are deposited in the Herbarium of the Florida Agricultural Experiment Station at Gainesville.





Figs. 2, 3. *Polyporus Westii* Murrill. Fig. 2, upper surface. Fig. 3, lower surface. Photos by A. S. Rhoads.

Gainesville, Fla., August 27, 1938 (*F18100*). Also collected by E. West near the same spot on a magnolia log, July 20, 1938 (*F17913*). A striking species decorated with sharp tufts of umbrinous fibrils and beautifully reticulate with brown lines.

*Polyporus Rhoadsii* sp. nov.

Pileo 6–8 cm. lato, squamuloso, ochraceo; poris parvis, ochraceis; sporis  $6 \times 3\mu$ ; stipite subglabro, fulvo,  $2-4 \times 1-1.5$  cm.

Pileus circular in general outline, depressed, about 6–8 cm. broad; surface conspicuously squamulose, dry, uniformly ochraceous, sometimes fulvous on drying; margin undulate to slightly lobed, fertile, concolorous, rarely deflexed in dried specimens; context white, soft-corky, homogeneous, 0.5–1 cm. thick; tubes short, decurrent, pallid to ochraceous or fulvous, mouths 3–4 to a mm., rather thin-walled, subcircular to angular, edges entire; spores pip-shaped, obliquely apiculate, smooth, hyaline, about  $6 \times 3\mu$ ; setae and cystidia wanting; stipe usually central, subequal, often flattened, subglabrous, avellaneous or fulvous to subfuliginous, white and firm to corky within, about  $2-4 \times 1-1.5$  cm.

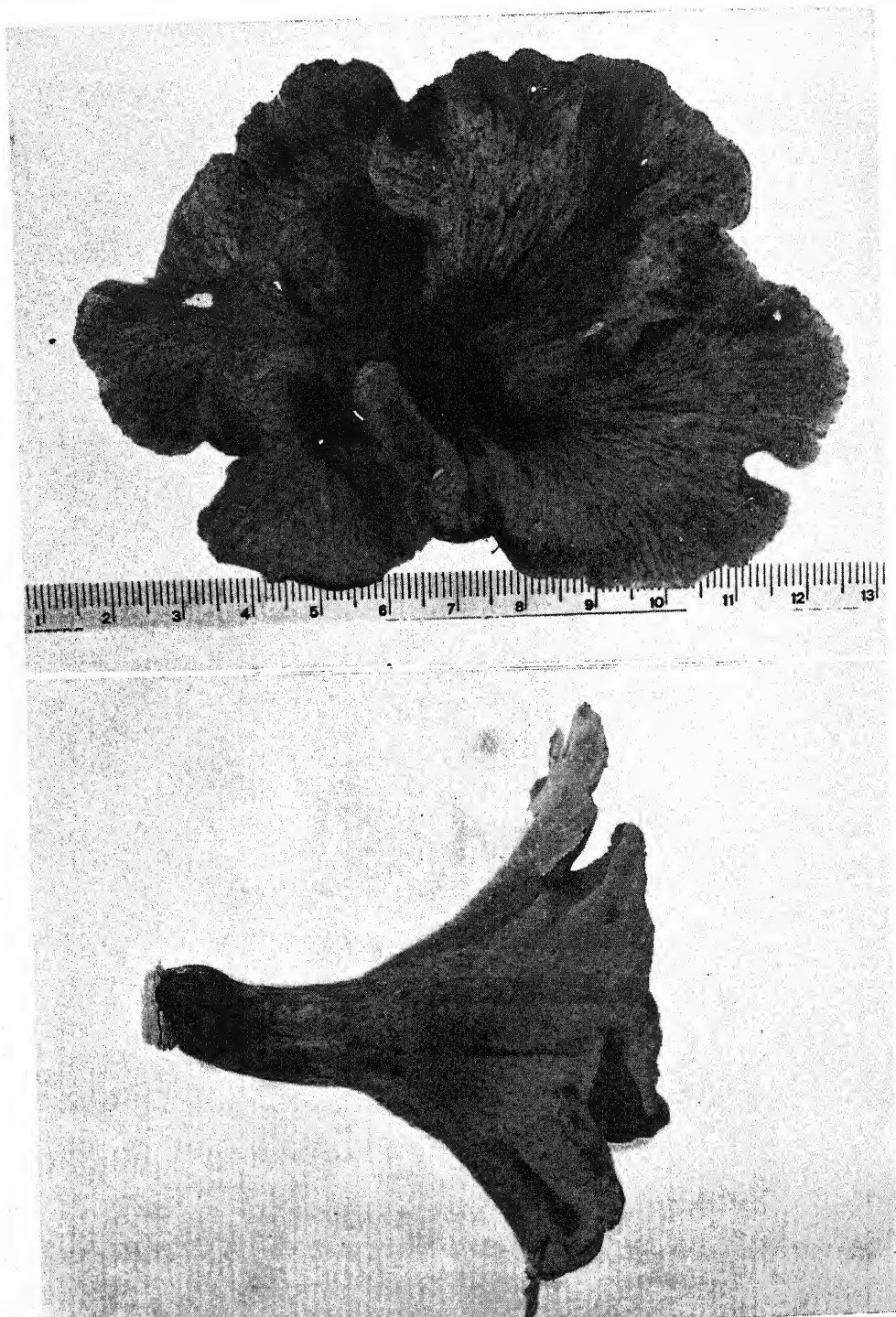
Type collected by A. S. Rhoads and Erdman West on an oak stump at Magnesia Springs, Alachua Co., Fla., August 16, 1935 (*F8938*). Also collected by Bratley and West on a rotten fallen pine branch at Magnesia Springs (*F8931*); and by J. R. Watson on buried wood near Gainesville (*F8948*). This last specimen is multiplex, two stems having grown together and the caps being quite irregular because of the union. The author found two sweet-gum logs covered with old hymenophores of this species on June 5, 1938 (*F16327*). In this aged condition the caps were virgate rather than squamulose, suggesting *P. virgatus*, a tropical species. Mr. West collected a fresh specimen on oak, June 19, 1938 (*F16379*), which yielded an abundance of spores.

*Polyporus Arnoldae* sp. nov.

Pileo umbilicato, caespitoso, 4–6 cm. lato, roseo-isabellino; tubulis prae-minutis, decurrentibus; sporis ellipsoideis,  $5-6 \times 3-4\mu$ ; stipite pallido, glabro,  $1.5-2 \times 0.5-0.8$  cm.

Pileus circular or subcircular, umbilicate, caespitose, 4–6 cm. broad; surface hygrophanous, subglabrous, pale rosy-isabelline; margin very thin, subentire or undulate, even, straight, sodden-white for 1 cm., eroded and slightly fissile with age, not ciliate; context thin, pallid, with pleasant odor and taste; tubes minute, thin-walled, decurrent, stramineous, the edges becoming eroded; spores ellipsoid, smooth, hyaline, copious,  $5-6 \times 3-4\mu$ ; stipe tapering downward, glabrous, smooth, solid, whitish with an avellaneous tint,  $1.5-2 \times 0.5-0.8$  cm.

Type collected by E. West, Lillian Arnold and W. A. Murrill on a



Figs. 4, 5. *Polyporus Rhoadsii* Murrill. Fig. 4, slightly enlarged to show virgate surface.  
Fig. 5, about natural size. Photos by A. S. Rhoads.

hardwood log in Planera Hammock, eleven miles northwest of Gainesville, Fla., July 16, 1938 (*F17863*). Suggesting *P. albiceps* Peck in some ways but deeply umbilicate, very thin, and not pure-white.

*Abortiporus subabortivus* sp. nov.

Pileo convexo-depresso, tomentoso, roseo-isabellino, 10–15 cm. lato; tubulis angulatis, brevibus, albis; sporis subglobosis, asperulatis, 5–6 $\mu$ ; stipite subglabro, pallido, 4–6 $\times$ 1–2.5 cm.

Convex to depressed, gregarious to subcespitose, 10–15 cm. broad; surface spongy, shaggy-tomentose, rosy-isabelline, somewhat zonate, margin thin, paler, broadly sterile; context thin, duplex, the upper layer loosely woven and concolorous, the lower firm, white, tough and flexible, odor pleasant, taste like wet wood; tubes decurrent, about 2 mm. long, 2–3 to a mm., angular, very thin-walled, edges mostly entire, white, usually turning dark-brown when dried; spores subglobose, thin-walled, hyaline, granular, minutely asperate, copious, 5–6 $\mu$ ; stipe subequal, often irregular, firm, corky, subglabrous, subconcolorous or pallid, often radicate, about 4–6 $\times$ 1–2.5 cm.

Type collected by West and Murrill on roots in Sanchez Hammock, eleven miles northwest of Gainesville, Florida, July 23, 1938, (*F17955*). Also collected by West and Murrill on roots in Kelley's Hammock, ten miles northwest of Gainesville, July 19, 1938 (*F17933*). In this latter collection the tubes were entirely sterile and there were also three aborted hymenophores. The species resembles *A. distortus*, but has a shaggy surface, a different context, and a firmer stem. The spores, instead of being usually ellipsoid and always smooth and uninucleate, are subglobose, granular and minutely asperate. The large sporophores spring from the ground over buried roots, to which they are attached.

*Hahalopilus subrutilans* sp. nov.

Pileo dimidiato, saepe effuso-reflexo, ochraceo, tomentoso; poris albis, minutis; sporis ellipsoideis, 3.5 $\times$ 2.5 $\mu$ .

Pileus imbricate, sessile, dimidiate, convex, often resupinate, the reflexed portion 2–3 $\times$ 3–6 $\times$ 1–1.5 cm.; surface ochraceous, sometimes fulvous on drying, conspicuously tomentose, azonate; margin thin, entire or lobed, subconcolorous, not deflexed on drying; context thin, soft-corky, homogeneous, isabelline; tubes slender, white, about 5 mm. long, mouths minute, 6 to a mm., slightly angular, the edges entire, thin, concolorous; spores ellipsoid, regular, smooth, hyaline, 3.5 $\times$ 2.5 $\mu$ .

Type collected by A. S. Rhoads on a fallen branch of *Magnolia glauca* at Hatchet Creek near Gainesville, Fla., Oct. 16, 1927 (No. *F8750*). This species is paler than *H. rutilans*, more inclined to be resupinate, and has much smaller tubes. Both species are rare in this locality.



*Corioloopsis Tisdaleana* sp. nov.

Pileo dimidiato,  $3 \times 6 \times 0.3-1$  cm., sulcato, tomentoso, ochraceo-ferruginoso; tubulis magnis, subhexagonis, sporis hyalinis,  $10 \times 4\mu$ .

Pileus gregarious, dimidiate, conchate, about  $3 \times 6 \times 0.3-1$  cm.; surface narrowly concentrically sulcate, conspicuously tomentose, ochraceous-ferruginous, fulvous behind; margin straight, rather thin, ochroleucous, entire to undulate or slightly lobed, with a narrow white sterile border below; context tough, flexible, isabelline, 2-3 mm. thick, odor and taste not characteristic; hymenium pallid, then avellaneous-isabelline, unchanged on drying; tubes large, hexagonal or subhexagonal, 1-2 to a mm., the edges firm, medium thick and entire; spores oblong-ellipsoid, smooth, hyaline, granular, copious, about  $10 \times 4\mu$ ; cystidia none.

Type collected by West and Murrill on a dead hardwood log in Sanchez Hammock, eleven miles northwest of Gainesville, Florida, July 23, 1938 (F17975). Dedicated to Dr. W. B. Tisdale, Chief Plant Pathologist in the Experiment Station.

*Trametes Humeana* sp. nov.

Pileo dimidiato, 7-10 cm. lato, albo, anisato; sporis ellipsoideis, hyalinis,  $3 \times 2\mu$ .

Pileus dimidiate to reniform, narrowly to broadly sessile, rarely imbricate, 5-7  $\times$  7-10  $\times$  1.5-3 cm; surface anoderm, opaque, uneven, pruinose, slightly zonate at times, white to partly rosy-avellaneous, slightly rosy-avellaneous behind in young specimens becoming darker with age; margin thin, entire or undulate, very narrowly sterile; context tough, fibrous, concentrically zonate, pallid, with nutty flavor and a strong odor of anise, about 7 mm. thick, becoming slightly rosy-avellaneous after being cut; hymenium even, white, rosy-avellaneous where bruised; tubes about 7 mm. long, white within, slightly rosy-avellaneous when cut, mouths angular, 2 to a mm., at times irregularly elongate and daedaleoid, edges thin, entire; spores broadly ellipsoid, smooth, hyaline, uniguttulate, about  $3 \times 2\mu$ .

Type collected by West and Murrill on a dead oak log under hardwood trees in Sugarfoot Hammock, near Gainesville, Fla., August 4, 1938 (F17978). Suggesting *Tyromyces Spraguei* (Berk. & Curt.) Murrill, but differing in color, context, odor and size of spores. Dedicated to Dr. Harold H. Hume, Director of Research at the Florida Agricultural Experiment Station.

*Trametes subcubensis* sp. nov.

Pileo applanato, dimidiato, lato, sulcato, albo vel cremeo; tubulis 1 cm. longis; sporis  $6 \times 3\mu$ , cystidiis nullis.

Pileus dimidiate, applanate, 6-10  $\times$  10-20  $\times$  1-2 cm.; surface anoderm, uneven, rugose, somewhat sulcate, subglabrous, white or cremeous, margin



entire to lobed, concolorous, ochraceous behind; context white to yellowish, soft, punky, with the odor of anise, 5-10 mm. thick; tubes corky, 4 to a mm., reaching at least 1 cm. long, mouths subcircular, entire, pallid to creameous; spores elongate, smooth, hyaline, copious, about  $6 \times 3\mu$ ; cystidia none.

Type collected by W. A. Murrill on an oak log at Magnesia Springs, Alachua Co., Fla., May 22, 1938 (F16240). Also collected by the author on an oak log at Gainesville, Fla., April 6, 1938 (F16191). Suggesting *T. cubensis* (Mont.) Sacc. but having much longer tubes, an anoderm surface, and elongate spores.

***Tyromyces avellaneialbus* sp. nov.**

Effuso-reflexo, avellaneo; poris parvis, albis, angulatis; sporis subglobosis,  $3\mu$ .

Effused for several centimeters with narrowly reflexed margin, somewhat imbricate, the reflexed portion  $1-2 \times 2-4 \times 0.2-0.7$  cm., wider by confluence; surface dry, uneven, pubescent, azonate, avellaneous, margin even, lobed, concolorous; context milk-white or pallid, unchanging, 2-3 mm. thick, taste astringent, somewhat like that of the toothache tree; tubes snow-white, 2-3 mm. long, mouths circular and thick-walled to angular and thinner-walled, glistening, white, with a faint greenish tint, 3-4 to a mm., edges entire; spores very copius, subglobose to broadly ovoid, smooth, hyaline, uniguttulate, about  $3\mu$  long; cystidia none.

Type collected by W. A. Murrill on a sweet-gum log at Newnan's Lake, Alachua County, Florida, May 1, 1938 (F15621). A very distinct species, found but once. The name refers to the uniformly avellaneous surface and the milk-white hymenium.

***Coriolus membranaceus taxodii* var. nov.**

Pileo dimidiato, imbricato, zonato, pallido et fumoso; poris albis, parvis; sporis  $4-5 \times 2.5\mu$ .

Pileus dimidiate, densely imbricate,  $3-5 \times 5-10 \times 0.2-0.3$  cm., often laterally confluent; surface zonate, pubescent to glabrous, usually rough behind and plicate with age, whitish or creameous with fumous zones; margin thin, fumous, entire to undulate or lobed; context thin, white, tough; tubes 1 mm. long, white, creameous on drying; mouths glistening, angular, thin-walled, entire, 3-4 to a mm., often irregular and dentate with age; cystidia none; spores copius, oblong-ellipsoid, smooth, hyaline, nonguttulate, about  $4-5 \times 2.5\mu$ .

Type collected by W. A. Murrill on dead cypress logs at Newnan's Lake, Alachua County, Florida, April 24, 1938 (F8598). Growing in very densely imbricated masses on the ends of logs lying in boggy places. The peculiar dark-gray color of the zones and margin is distinctive in younger stages but may disappear with age. Black cypress is the only host.

*Coriolus subabietinus* sp. nov.

Effuso-reflexo, 1-5 cm. lato, fibrilloso, pallido; poris albidis, minutis, angulatis.

Effused in patches 1-5 cm. broad, narrowly reflexed, margin incurved on drying; the reflexed portion very thin, densely fibrillose, even, pallid, undulate to lobed; context watery-pallid, membranous; tubes short, less than 1 mm., pallid within, mouths whitish to cremeous, angular, about 5 to a mm., edges entire, becoming rather thin at maturity; cystidia none; spores not found.

Type collected by Erdman West and W. A. Murrill on a pine log at Gainesville, Florida, October 24, 1932 (F8746). The tubes are too small for *C. abietinus*. A few spores were found which were globose, smooth, hyaline, 3-4 $\mu$ , but their origin was uncertain.

*Coriolus sublimitatus* sp. nov.

Pileo imbricato, 2-4 cm. lato, sulcato, tomentoso, pallido; poris albis, minutis, angulatis.

Pileus imbricate, flabelliform, sessile, thin, coriaceous, flexible, 2-4 cm. broad; surface concentrically sulcate, tomentose, pallid to grayish; margin white to isabelline, subentire, thin, broadly sterile, incurved on drying; context thin, fibrous, firm, pallid; tubes short, white, mouths minute, angular, edges thin, subentire; spores not found; cystidia wanting.

Type collected by A. S. Rhoads on a dead citrus trunk at Indianola, Florida, January 4, 1929 (F8741). This species differs from *C. limitatus* in being densely imbricate and in having white instead of reddish tubes.

*Coriolus tenuispinifer* sp. nov.

Pileo conchato, 2 cm. lato, albo, tomentoso, sulcato; poris parvis, albidis; cystidiis longis, rubro-brunneis, 100-125 $\times$ 3-6 $\mu$ .

Pileus very thin, conchate, sessile, gregarious, not imbricate, reaching 1 $\times$ 2 cm.; surface uniformly white and villose-tomentose, concentrically sulcate, margin subentire, deflexed on drying; context very thin, white; tubes short, irregular, angular, thin-walled, white to isabelline, about 4-5 to a mm., edges soon becoming dentate; spores not found; cystidia abundant, long, slender, straight or flexuous, dark reddish-brown, slightly tapering upward from a slightly enlarged base, acute but not sharp at the tip, which is usually subhyaline, 100-125 $\times$ 3-6 $\mu$ .

Type collected by W. A. Murrill, G. F. Weber and Erdman West on a decayed fallen oak branch in mixed woods at Gainesville, Florida, December 1, 1926 (F8755). Found but once. Resembling *C. depauperatus* (Pat.) Murr., but having slender spines on the hymenium.

*Fomitiporia punctatiformis* sp. nov.

Late effuso, 7 mm. crasso, margine isabellino, adnato, 1 cm. lato; poris minutis, avellaneo-umbrinis.

Broadly effused, extending many centimeters along branches, inseparable, elongate-elliptic, rigid, about 7 mm. thick; margin isabelline to lateritious, and finally bay or chestnut with age, adnate, rather thick, subglabrous to glabrous, about 1 cm. broad; context inconspicuous; hymenium smooth, convex, somewhat glistening, several times indistinctly stratified; tubes about 7 mm. long, whitish-stuffed, avellaneous-umbrinous within, mouths regular, minute, circular, 6 to a mm., edges thick, entire, avellaneous-umbrinous; cystidia none; young spores globose, smooth, hyaline,  $2-3\mu$ .

Type collected by A. S. Rhoads on a dead fallen oak branch in a hammock west of Cocoa, Fla., June 10, 1937 (*F12073*). Suggesting *F. punctata*, but the tubes are not distinctly stratified.

*Poria alachuana* sp. nov.

Effuso, 2-4 mm. crasso, margine albo; poris albis, angulatis, parvis; sporis ovoideis,  $3-4 \times 2-3\mu$ .

Effused, continuous, inseparable, 2-4 mm. thick, often reviving and stratified; margin thin, milk-white, mostly evanescent; context thin, white, scarcely apparent in age; hymenium rather uneven, somewhat glistening, white to lemon-yellow; tubes angular, irregular, thin-walled, entire, 4-5 to a mm., or larger by confluence; spores ovoid, smooth, hyaline,  $3-4 \times 2-3\mu$ ; cystidia none.

Type collected by W. A. Murrill on a decayed hardwood log in Prairie Creek Hammock, Alachua Co., Fla., Mar. 27, 1938 (*F16157*). Found but once. In older dried specimens the hymenium cracks into areas one or two centimeters long.

*Poria Floridae* sp. nov.

Effuso, 2-3 mm. crasso, margine albo; poris pallidis, minutis, angulatis; sporis globosis,  $3\mu$ .

Effused for several centimeters, continuous, inseparable, about 2-3 mm. thick; margin inconspicuous, delicate, milk-white, mostly disappearing with age; context white, thin, scarcely apparent in old specimens; hymenium fairly even, dull-white to dull-pale-rosy-isabelline; tubes minute, nearly regular at first, thin-walled, angular, entire, about 7-8 to a mm., becoming more or less unequal, elongate at times, or enlarging by the splitting of the walls; spores globose, smooth, hyaline,  $3\mu$ ; cystidia none.

Type collected by W. A. Murrill on a hardwood log in a low hammock at Gainesville, Fla., Mar. 25, 1938 (*F16121*). Found but once. Some parts of the hymenium show one or two indistinct lines of stratification, indicating seasonal growth.

*Poria ferruginicincta* sp. nov.

Late effuso, 1-1.5 cm. crasso, margine ferrugineo; poris albis ad subbrunneis, minutis; sporis subglobosis,  $5\mu$ .

Widely and almost continuously effused, inseparable, about 1-1.5 cm. thick; margin narrow, undulate, ferruginous; context white, thin, scarcely apparent at maturity; hymenium uneven, white to brownish-discolored; tubes regular, thin-walled, angular, entire, about 5-6 to a mm., becoming quite irregular in shape and size; spores subglobose, smooth, hyaline, about  $5\mu$ ; cystidia none.

- Type collected by Erdman West and W. A. Murrill on an oak log at Gainesville, Fla., Nov. 7, 1932 (F9127). A large, coarse, more or less undulate species, white when fresh but brown in the herbarium.

*Poria holoseparans* sp. nov.

Effuso interrupto, 1-2 mm. crasso, margine albo; poris albidis, valde minutis, angulatis; sporis globosis,  $3-4\mu$ .

Effused in patches several centimeters long and wide, not continuous, separable, 1-2 mm. thick; margin narrow, milk-white; context white, thin but substantial and remaining plainly visible; hymenium very even, sodden-white, whiter and somewhat glistening at maturity and becoming dirty-ochraceous with age; tubes minute, angular, regular, thin-walled, entire, about 10 to a mm.; sometimes larger; spores globose, smooth, hyaline, uniguttulate,  $3-4\mu$ ; cystidia none.

Type collected by W. A. Murrill on a wet hornbeam log in a low hammock at Gainesville, Fla., Apr. 8, 1938 (F16186). The hymenophores may curl up in drying and entirely separate from the substratum, suggesting a resupinate form of a pileate polypore.

*Poria lacteimicans* sp. nov.

Effuso, 1 mm. crasso, margine albo; poris albis, angulatis, valde minutis; sporis globosis,  $2\mu$ .

Effused for several centimeters, continuous, inseparable, about 1 mm. thick; margin very thin and delicate, milk-white; context thin, white, scarcely noticed in age; hymenium even, not stratose, glistening, milk-white, slightly brownish where bruised; tubes short, regular, angular, thin-walled, entire, very minute, about 10 to a mm.; spores copious, globose or subglobose, smooth, hyaline,  $2\mu$ ; cystidia none.

Type collected by W. A. Murrill on an oak log at Gainesville, Fla., Apr. 9, 1938 (F16199). Found but once. A dainty white species with very glistening hymenium.

## NEW COMBINATIONS

For the convenience of those using Saccardo's nomenclature, the following new combinations are made:

ABORTIPORUS SUBABORTIVUS = *Polyporus subabortivus*  
CORIOLOPSIS TISDALEANA = *Polyporus Tisdaleanus*  
CORIOLUS SUBABIETINUS = *Polystictus subabietinus*  
CORIOLUS SUBLIMITATUS = *Polystictus sublimitatus*  
CORIOLUS TENUISPINIFER = *Polystictus tenuispinifer*  
FOMITIPORIA PUNCTATIFORMIS = *Poria punctatiformis*  
HAPALOPILUS SUBRUTILANS = *Polyporus subrutilans*  
PYROPOLYPORUS TAXODII = *Fomes taxodii*  
TRAMETES HUMEANA = *Polyporus Humeanus*  
TRAMETES SUBCUBENSIS = *Polyporus subcubensis*  
TYROMYCES AVELLANEIALBUS = *Polyporus avellaneialbus*

HERBARIUM, FLORIDA AGRICULTURAL EXPERIMENT STATION  
GAINESVILLE, FLA.



## INDEX TO AMERICAN BOTANICAL LITERATURE

The aim of this Index is to include all current botanical literature written by Americans, published in America, or based upon American material; the word America being used in the broadest sense.

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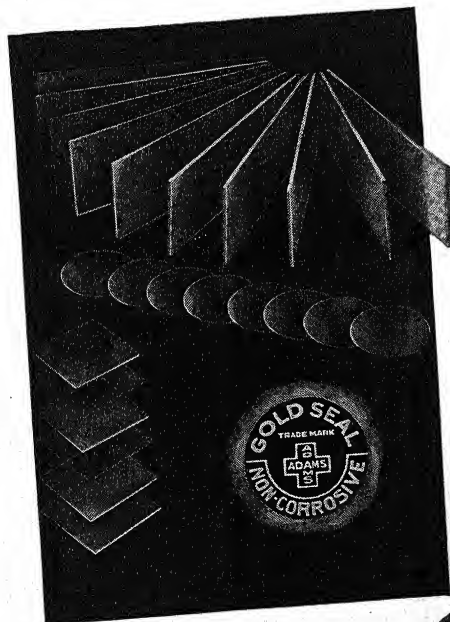
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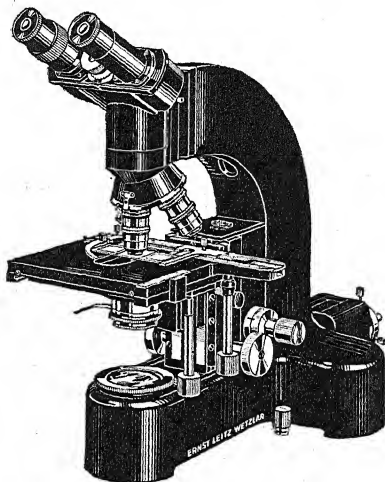
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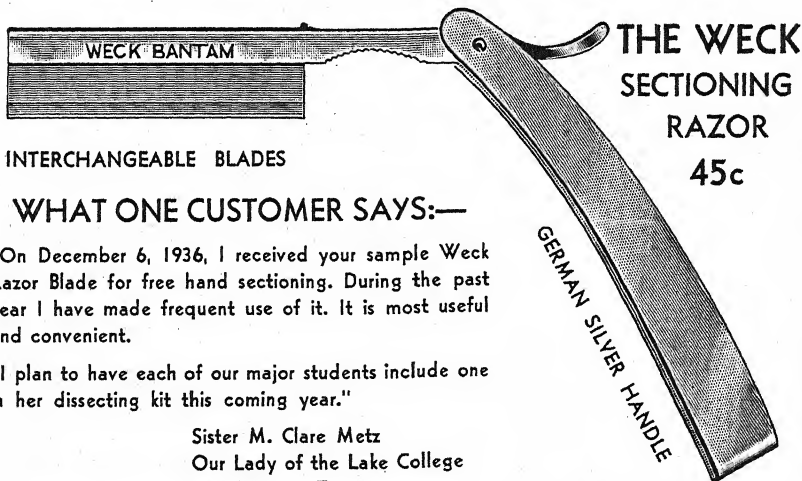


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